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# Factors influencing guanaco habitat use and group size in Torres del Paine National Park, Chile

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by

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# ABSTRACT

Selection of preferred vega habitat by family group and solo male guanacos was studied on 14 sites in Torres del Paine National Park, Chile during 7 2-week sampling intervals from 1 November to 15 February. Vegas were chosen such that 7 were dominated by family group territorial males and 7 were defended by solo territorial males. Of 32 territorial males observed on the 14 sites, 17 were family group territorial and 15 were solo males. Average group sizes ranged from 1 for solo males to 5 for family group males. Forage related and site physical characteristics were quantified and analysis of variance was used to test for differences between family group and solo male vega sites. Correlation analysis was used to examine potential relationships between vega characteristics and the degree of family group use. Vega physical and forage characteristics were both related to number of females, and may both impact guanaco populations through their influences upon predation of guanacos by pumas and guanaco foraging efficiency, respectively. Female guanacos probably selected vega habitat over all other available types based upon forage nutritional characteristics. However, female selection among particular vegas was most likely mediated by both site physical and forage characteristics. The characteristics

most related to female use of vegas were grazing use during the previous month, vega surface area, and vega perimeter. Other variables appreciably related to female use were unit standing crop, unit productivity, forage moisture content, meters of periphery possessing slopes $\geq$ 20%, PCI (an index of risk to predation), unit standing DDM, and plant maturity. Percent occurrence of Eleocharis pachycarpa, a small sedge, was also weakly related to female use. No significant relationships were established between use of vegas by females and absolute or percent meters of cover or slope located at a vega periphery. Additionally, no relationships were observed between female use and percent peripheral slope per unit area, vega total productivity of caged vegetation, vega total grazed standing crop, plant height, forage availability index (plant height x vega area), percent crude protein, standing crop crude protein, percent dry matter, total standing dry matter, and species composition of Carex gayana, Holcus lanatus, Agrostis capillaris, Hordeum comosum, or Potentilla anserina. Predation and forage/nutrition related factors must be investigated simultaneously in trying to understand trade-offs that ungulates (as prey) must deal with to survive in a complex and interactive ecological environment.

# INTRODUCTION

Predator and forage related factors are recognized as major determinants of habitat selection and group size in wild populations because they can influence animal distributions and movements (Wilson 1975, Barash 1982, Peek 1986, Krebs and Davies 1987). Physical factors can influence animal populations through mechanisms associated with protection cover, thermal cover, and predation (Hornocker 1970a, Peek 1986). Forage characteristics can influence animals through mechanisms of foraging efficiency, forage resource limitation, and competition (Wilson 1975, Krebs and Davies 1987). Costs and benefits resulting from animal responses to predation and foraging/nutritional pressures are important in understanding trade-offs that animals must make in order to survive (Jarman and Sinclair 1979, Maddock 1979, Sinclair 1985). Models indicate that the two factors must be examined simultaneously in order to understand ecology of animal populations (McNamara and Huston 1987).

Habitat selection by, and group size in the guanaco (Lama guanicoe) in southern Chile may be determined by forage characteristics, habitat characteristics, and predation related or social factors (Jefferson 1980, Franklin 1983, Ortega and Franklin 1988). Social factors

can be interpreted as responses to pressures related to feeding or predation (Wilson 1975, Barash 1982, Franklin 1982). Social system dynamics are important in understanding guanaco ecology (Franklin 1983). Guanaco social organization consists of 5 social units: Family Groups (FGs), Male Groups (MGs), Solo Males (SMs), Mixed Groups (MXGs), and Female Groups (FEGs) (Franklin 1982). FGs (the reproductive unit), and MGs (future breeding males) form the foundation of guanaco populations. All 5 social units occur in Torres del Paine National Park (TPNP) in southern Chile (Ortega and Franklin 1988).

Four periods of guanaco social and ecological interaction were identified by Ortega and Franklin (1988). These are: winter-aggregational, spring-transitional, summer-territorial, and fall-transitional. Guanacos at TPNP migrate east to west during the fall-transitional and winter-aggregational socioecological periods, possibly in response to snow cover, forage availability, predation, and thermal regulation advantages. The guanaco mating system is based upon resource defense polygyny during the summer-territorial period when males defend territories encompassing high quality food resources to which females are attracted (Franklin 1982). Territoriality peaks during spring-transitional and summer-territorial periods when

parturition and mating occur (Jurgensen 1985, Ortega and Franklin 1988).

Females, theoretically, may be attracted to characteristics of specific territorial males (Jurgensen 1983). However, previous studies of "successful" males indicated that they defended higher quality resources than males failing to attract as many females. More females were attracted to "successful male" territories over time as a result of an increase in the amount and availability of quality vegetation as pond waters receded during the dry season (Jurgensen 1985). Therefore, we only considered environmental characteristics of guanaco territories in our evaluation of female habitat use.

Censuses at TPNP indicated that 94% of all females were seen in FGs during summer (Ortega and Franklin 1988). During the summer-territorial period, 63% of all males were in MGs, whereas only 16% were in FGs as Family Group Territorial Males (FGTMs), and 21% were Solo Territorial Males (STMs)(Franklin and Fritz, In Press). Of all males defending territories, 57% were STMs which failed to attract females due to either a shortage of females or an inability to defend habitat favored by females (Franklin and Fritz, In Press).

During spring and summer in TPNP, guanacos preferred a meadow vegetation type called "vegas" (Franklin 1978,

Jurgensen 1985, Ortega and Franklin 1988). Vegas are low lying meadows, ephemeral ponds, or littoral zones, all of glacial origin, that are capable of supporting and sustaining a rich variety of forbs and grasses (Pisano 1973, 1977, Moore 1983).

Vega use by guanacos during the summer-territorial period has exceeded 80%, even though it is the least available vegetation type in the park (Jurgensen 1985, Ortega and Franklin 1988). Female and chulengo (guanaco young) preference for vegas suggests that vegas may have high availability of succulent, nutrient rich vegetation (Jurgensen 1985). Male status as either a FGTM or STM is determined as females select vegas that are located within areas defended by territorial males. Although some females are occasionally rejected by territorial males, group size or group creation is the result of female site selection.

Despite its importance to guanacos, some vegas sustain little or no guanaco use during summer (W. L. Franklin, Dept. of Animal Ecology, Iowa State University, Ames, Iowa, pers. comm., G. Garay, Corporación Nacionál Forestál (CONAF), Puerto Natales, Chile, pers. comm.). Although "unused" vegas are often located within the territory or home range of a STM, their apparently ample resources fail to attract females, resulting in little or no FG usage of these sites. Two reasons why some vegas remain unused are

suspected. First, site-specific differences may influence vegetation quality or composition (McNaughton 1979, 1988). Territories defended by successful males that attract females should include resources of higher quantity and/or quality than those occupied by STMs. Second, "unused" vegas may occur within areas that possess physical characteristics that favor predation by the Patagonia puma (Felis concolor patagonica), the major predator of guanacos in TPNP (Wilson 1984, Cajal and Lopez 1987, Iriarte 1988).

## Objectives and Hypotheses

A unique opportunity existed at TPNP to examine how forage and physical habitat characteristics impact both habitat selection and group size in the guanaco. The goal of this study was to determine the major factors influencing preferred habitat selection and group size by guanaco FGs. Forage characteristics were species composition, quality, productivity, maturity, and availability of vega forages. Physical characteristics were vega area, perimeter, peripheral cover, and peripheral slope. The following hypotheses were tested:

1) No differences exist between vegas selected by females (FGTM vegas) and vegas not selected by females (STM vegas) with respect to means of plant species

composition, moisture, protein content, digestibility, maturity, availability, as well as vega productivity, size, perimeter, peripheral cover, and peripheral slope.

2) If means of variables differed significantly, then correlation analysis was used to identify the strongest relationships between forage and/or physical characteristics and the dependent variable, female vega use. Criteria used to assess the relative importance of forage or physical characteristics and their relationships with female vega use were correlation r-values, and probabilities of a greater test statistic.

# STUDY AREA

## Torres del Paine National Park

Torres del Paine National Park is located in the eastern foothills of the Andes mountains on the western edge of the Chilean Patagonia in the southern Chilean province of Magallanes (51° 03'S, 72° 55'W). The study area was located in the east-central section of the park and was bounded on the north and west by Lake Norsdenkjold, on the west by Lake Pehoe, and on the south by Lake Sarmiento. The eastern park boundary is fenced and borders a large sheep and cattle ranch (Fig. 1).

## Study Area

The peninsula-shaped study area consists of 2 guanaco-used regions based upon topography and use (Fig. 2). The eastern region (3250 ha), the main summer guanaco range (Ortega and Franklin 1988), is composed of gentle to moderately sloping landscapes of glacial origin. The area is dotted with numerous lakes, ponds, depressions, and vegas. The landscape slopes from north to south, from an abrupt ridge overlooking Lake Norsdenkjold and the Paine River valley, to Lake Sarmiento. The main slope is

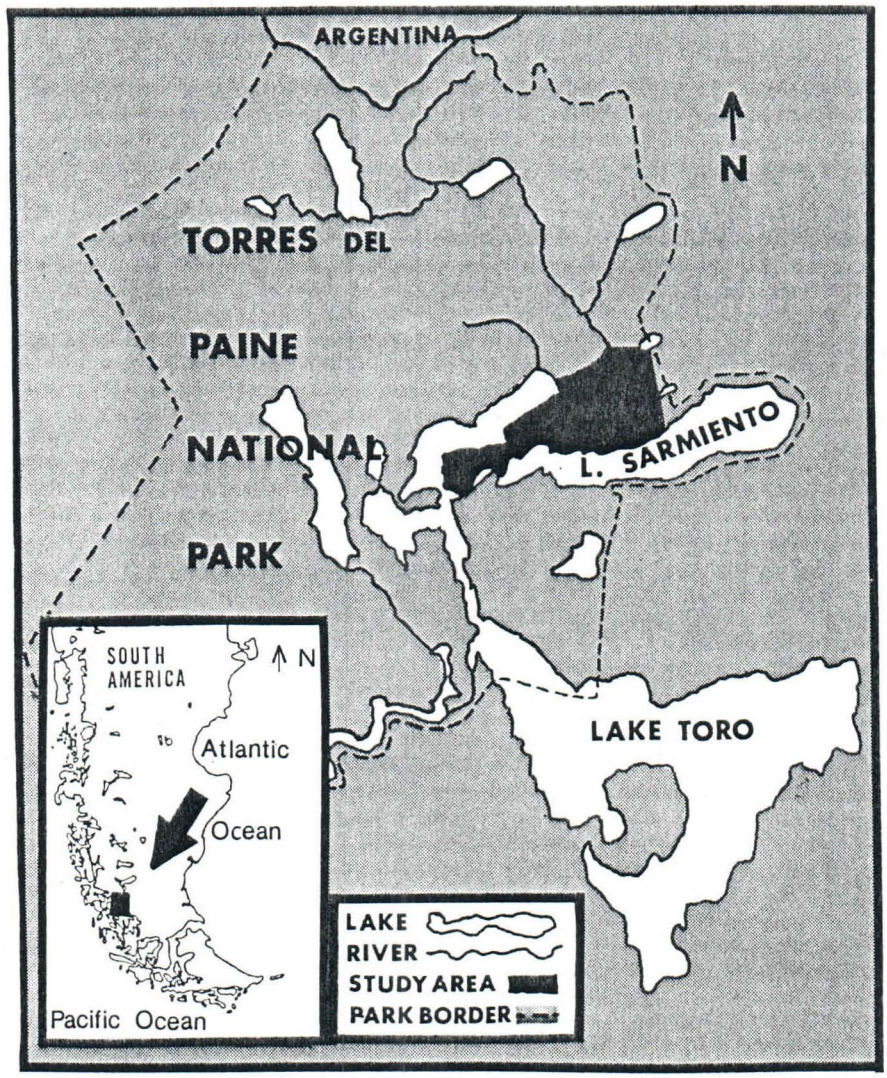


Figure 1. Map of Torres del Paine National Park, Chile, showing study area in black

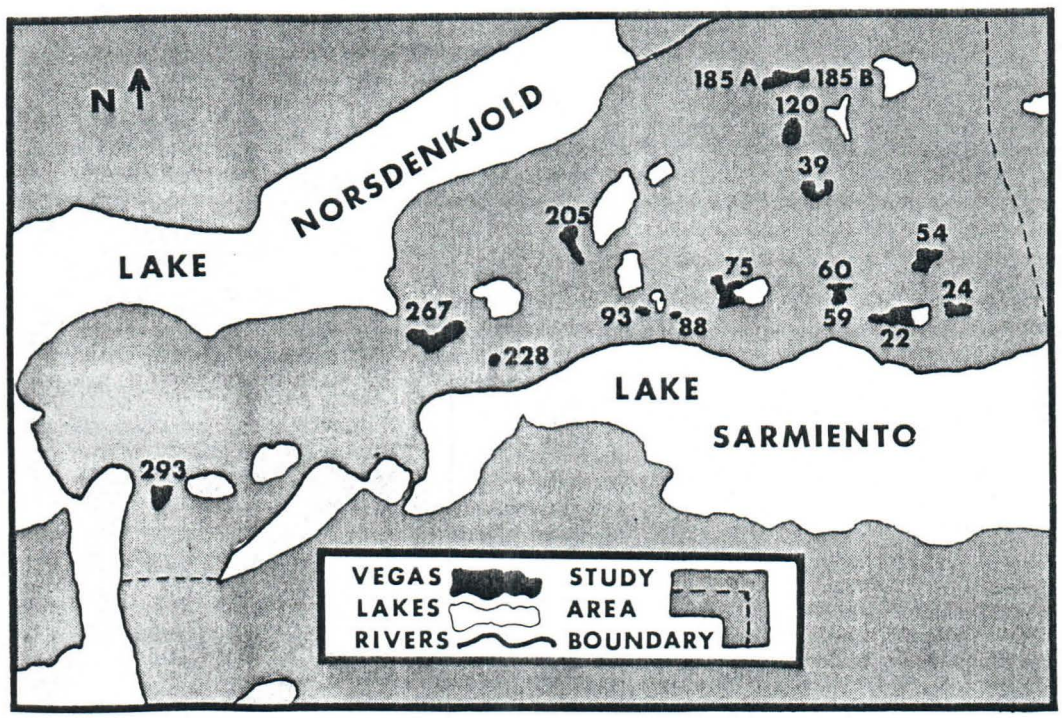


Figure 2. Map of study area showing locations of 14 study vegas. Sites designated by two numbers are a complex of two connected vegas

transected from northeast to southwest by gently to deeply etched ravines which may have served as watercourses between Lake Norsdenkjold and Lake Sarmiento during moister eras. A high density of lakes, ponds, and vegas occur in the eastern area, usually in association with these old watercourses.

The western region (2800 ha) comprises the guanaco winter range. This region is composed of high to moderate sloping landscapes, steep, rugged hills, and deep canyons. The same pattern of transecting watercourses found in the east is also observed in the west. Although less numerous, western watercourses generally retain greater quantities of water longer than those located on the eastern half of the peninsula. In addition, topography associated with western watercourses is severe. As in the east, most lakes, ponds, and vegas occur in valleys of major watercourses.

## Summer Weather

Summer weather at TPNP is variable, accompanied by moderate to high velocity winds that sweep off of the Paine mountain massif to parch the arid foothills of the study area. The Paine peaks produce a rain shadow from west to east across the peninsula. Average annual precipitation ranges from approximately 600 mm at Lake Pehoe in the west to 400 mm in the region of the eastern park boundary

(Armesto et al. 1988). Sixty percent of the annual precipitation generally falls from January to May. Summer average temperatures range from 4.0° to 16.1°C in the cooler, western region of the park. Summer daily temperature variation can be extreme, with changes of as much as 15°C observed (Park Meteorological Records 1970-1988, J. Gonzalez, CONAF, Puerto Natales, Chile, pers. comm.).

## Vegetation

The vegetation of the study area is characterized as a "xeric pre-Andean associatión" ("asociación matorrál xerofito pre-andino")(Pisano 1974). Six vegetation types within this association were identified by Ortega and Franklin (1988). Mata Barrosa is an upland shrub community comprising 41% of vegetation cover in the study area. It is dominated by Mulinum spinosum, a low-growing, dome-shaped, spiny shrub. Coirón is an upland community dominated by Festuca gracillima from whence this community is named. It composes 29% of all vegetation cover. Hierbas is an upland, forb dominated community composing 24% of the area. Vega, or the meadow community makes up only 4% of the peninsula, but is the most preferred type (Ortega and Franklin 1988). It is composed mainly of sedges, grasses, and forbs. Nirre

is the southern beech (Nothofagus antarctica) dominated "forest" community composing 2% of the area. Calafate (Berberis buxifolia), a spiny shrub that grows 1-2 m high, dominated the low-lying community of the same name which composes the remaining 1% of the study area.

# METHODS

The study was conducted from late October 1987 until mid-February 1988 between the killing frosts of that year. Some FGs had already begun to form by mid-October, but the population was still in the spring-transitional socioecological period at that time (Ortega and Franklin 1988).

A group of ultimate factors potentially influencing guanaco selection of preferred habitat and group size were developed from forage and topographic physical characteristics developed by Peek (1986) and Krebs and Davies (1987).

## Vega Selection

Seven FGTM and 7 STM vegas were randomly selected from all vegas known to be defended by territorial males (approximately 300 of a total 365 vegas on the peninsula). Pre-designation of territories as either FGTM or STM was based upon past observations of guanaco-selected sites by Proyecto Puma personnel during monthly bird and guanaco censuses conducted since 1984 (G. Garay, CONAF, Puerto Natales, Chile, pers. comm.). FGTM and STM vegas for this study were classified as vegas that had a predominant

history of FG or SM use, respectively, during the three previous summer-territorial periods. Study vegas were selected with the constraint that their associated territories did not include other vega study sites.

## Vega Utilization and Guanaco Group Size

Seven biweekly censuses were conducted over a 2-day period between 0900 and 1800, when guanacos were found feeding on territories (Franklin 1982, 1983). Vega use was classified as either STM or FGTM depending upon the most frequently observed ( $\geq$ 50%) social unit on the site. Territorial boundaries were estimated at each site by observing agressive and marking behavior of territorial males from December to February (Franklin 1978, Jurgensen 1985). Territorial males were individually identified by ear tags, natural markings, scars, and behavioral traits (Fritz 1985, Jurgensen 1985, Franklin et al. 1989, unpubl. rept.). Each territory was initially observed for a minimum of 2 days (16 hours) and any remaining ambiguous territorial boundaries defined during subsequent censuses. Territories were observed between 0700 and 1900 for a total of 250 hours for the 14 study vegas.

Mean FG use of study vegas was calculated as the proportion of all sightings that a FG was seen on a given

vega. Female-days use (FDU) was calculated as the mean of the product of the average number of females seen on a vega during a 2-week census interval and the total number of days in that interval (14), calculated for each vega.

Vegas were classified roughly based upon the wetland classification system described by Cowardin et al. (1979). Site-specific modifiers were added to the basic system of classifying areas as either riverine, lacustrine, or upland.

## Forage Characteristics

### Species composition

Vega species composition was determined by using a loop-frequency technique in December when the majority of plants were mature and easily recognized (Gysel and Lyon 1980). Transect lines were located from the center of each vega and ran along randomly selected azimuths. One-half of all available points spaced 1 m apart on each transect were randomly selected, at which 0.1-$m^2$ loops were placed. The number and length of transects, therefore, varied with vega size. Transects were randomly placed until 185 loops were located. The number of loops adequately reflected species composition because few, if any, new species were recorded when more than 185 loops were used. Presence or absence of all plant species was noted and percent absolute occurrence was determined for each vega. Relative occurrence of

species over all vegas was calculated to determine species composition over all 14 study vegas, but was not used in either analysis of variance or correlation analysis.

Forage quality: Crude protein and digestible dry matter

Samples of known guanaco forage species were collected monthly from November-February to measure nutritive quality of forages by site. Browse species, mata barrosa and calafate, were included because of their abundance at vega edges (Pisano 1974, Jurgensen 1985, Ortega and Franklin 1988). Graminoids, Agrostis capillaris, Carex gayana, Deschampsia caespitosa, Eleocharis pachycarpa, bluegrass (Poa spp.), and coiron (Festuca spp.), were selected because of their dominance of relative occurrence on all 14 sites, and by their occurrence in guanaco diets (Raedeke 1980, R. K. Lawrence, Dept. of Range and Wildlife, Texas Tech, unpubl. data). Samples were collected from several individually rooted plants of each species until approximately 50 g was collected. Samples were weighed, stored in paper bags, and allowed to air-dry.

Samples were oven dried to constant weight at 45°C, ground through a 20 mesh (1-mm) screen in a Wiley Mill, and stored in air tight bottles. Samples were tested for digestible dry matter (DDM) by using the two-stage acid-pepsin technique (Tilley and Terry 1963). Crude protein (CP) was determined by using the modified Kjeldahl procedure

(Horwitz 1980). Percent CP and DDM values of all species were averaged to obtain overall forage CP and DDM percentages for each vega.

Forage quantity: caged vegetation

An index of forage productivity was determined by measuring total above-ground standing crop protected from grazing. Since this approach was not a true measure of total production under herbivory, it was interpreted as an index of productivity for each vega. Five 1.5-$m^2$ circular plots were located from the center of each vega by using randomly generated locations and azimuths. Plots were enclosed with cages immediately after the final killing frost in late October, and clipped from 22-25 January. Vegetation was clipped after anthesis but before major senescence, when most plants were still green and viable. Only the center 1 $m^2$ of each cage was clipped to avoid edge growth influence of cages. Plants were clipped at ground level and collected in plastic bags. Litter and other senescent material from the previous year were removed. Samples were weighed wet and dry, moisture contents were determined by subtraction, and were analyzed as a percentage of wet weight. Productivity (standing crop) estimates are reported on a dry weight basis. The mean of the 5 cages in each vega was called unit productivity, and the product of

unit productivity and vega area was called vega total productivity.

Forage quantity: uncaged vegetation

Five 1-$m^2$ plots per vega were clipped in November, and 10 in December to determine unit and total standing crop, standing CP, and standing DDM of unprotected, potentially grazed vegetation. Forage availability, maturity, and grazing use was estimated on each vega during two-week intervals from November-February. Four 12-m transects were located radiating away from each cage in the four cardinal directions. At 1-m intervals, vegetation height, flowering, and grazing use were noted. The resulting three measurements were indices of: 1) the amount of plant material available to animals at the beginning of the next time interval, 2) the proportion of mature plants, and 3) the proportion of grazed plants on the vega, respectively.

## Physical Characteristics

An analysis was conducted on predation data from Iriarte's (1988) study of pumas in Torres del Paine National Park. This was done to better illustrate potential functional relationships between vega physical characteristics, puma predation upon guanacos, and guanaco use of vegas. Vega total areas were calculated from their

lengths and widths by using trigonometry. Perimeters were directly measured by circumscribing vega peripheries with a measuring wheel. Peripheral cover was defined as any object located within 15 m of the vega periphery that visually obstructed a Robel stick ≥ .5 m in height. Cover primarily included vegetation and boulders. Peripheral slope was defined as any area occurring within 15 m of the vega periphery that contained a slope ≥ 20% (about 10°). Fifteen meters is considered an effective attack distance for pumas (Young 1946, Russell 1978, Anderson 1983). Slopes were determined by using an Abney level. Portions of each vega's periphery that met peripheral cover and slope criteria were measured with a measuring wheel and expressed both as the absolute number of meters and as a percentage of the total vega periphery.

Peripheral cover and slope expressed as either absolutes or percentages would not be good predictors of guanaco high-risk habitat with respect to puma predation. Vegas differ in size and area, and guanacos using large areas are in less contact with vega periphery than guanacos in small vegas. Predation risk would be directly proportional to peripheral slope and cover (absolute or percent), and inversely proportional to vega area. Thus, indices of risk from peripheral cover and peripheral slope were calculated as follows: Peripheral Cover Index (PCI) =

% peripheral cover/(vega area/area of largest study vega); Peripheral Slope Index (PSI) = % peripheral slope/(vega area/area of largest study vega). Vega area, in the denominator, was divided by size of the largest vega analyzed in order to relativize the index among vegas of different size.

## Analysis and Statistical Procedures

Data for foraging and physical variables were of two types: Class I--those collected on a repeated basis through the summer, such as availability and digestibility, and Class II--those for which one value per vega was obtained, such as area and perimeter. The experimental design for Class I variables included 14 vegas, 2 vega types (FGTM and STM), and 4 repeated measures. Class I variables were analyzed as a standard split-plot design with vega types (FGTM and STM) designated as the main effect and months (Nov.-Feb.) designated as the split-plot effect. Conservative degrees of freedom were used to determine probabilities associated with the F-statistic because of potential auto-correlation of monthly repeated measures (Cochran and Cox 1957). Class II variables were analyzed as a completely random design.

Two major approaches were used in the analysis.

First, t-tests were used to test for habitat differences between female-selected and female-unselected habitats (FGTM vs STM vegas, respectively). Analysis of variance (ANOVA) using the general linear models procedure of SAS was employed to investigate monthly trends and to test for interactions between trends and the two vega types, FGTM and STM (SAS Institute Inc. 1985). T-tests, and F-tests for analysis of variance were declared marginally significant at the 0.10 probability level, significant at the 0.05 probability level, and highly significant at the 0.01 level or below.

Second, correlation analysis was used to identify the strongest relationsips between independent variables that were significant in t-tests or ANOVAs and female days use of vegas. Relative importance of marginal ($P \leq 0.10$), significant ($P \leq 0.05$), and highly significant ($P \leq 0.01$) correlations were examined by comparing intensities of correlation (correlation coefficients) among independent variables. Treatment of inter-correlated independent variables ($r \geq 0.60$) is discussed in the results section.

# RESULTS

## Vega Selection

Six lacustrine, 3 riverine, and 4 upland vegas were selected for this study (Table 1, Fig. 2). While upland vegas were the most numerous vega type, they were usually small and did not meet the selection criteria for FGTM and STM study vegas. Lacustrine and riverine vegas were chosen in rough proportion to their total occurrence in the study area (Lawrence and Franklin ms in preparation).

## Vega Utilization and Guanaco Group Size

Territorial males and female guanacos used vega habitat more frequently than all other vegetation types combined. Of all guanaco sightings recorded during the 7 censuses (2063), 60% of territorial males ($X^2 = 19.33$, d.f. = 1, $P < 0.001$) and 85% of females ($X^2 = 119.6$, d.f. = 1, $P < 0.001$) were on vegas.

Of the 14 vegas that were preassigned either to FGTM or STM categories, none were classified incorrectly. FG use followed expectations, with FGs sighted on FGTM vegas more than on STM vegas (Table 2). Sometimes other males (most often SMs) defended a territory that included (excised) a

Table 1. Identification, surface area, and classification type of 7 FGTM vegas and 7 STM vegas in Torres del Paine National Park, Chile. Vegas with 2 identification numbers were composed of two connected vega sites

| Vega Name | Identification Number | Area (ha) | Classification |
|---|---|---|---|
| FGTMV | | | |
| Blanca | 120 | 8.34 | Xeric lacustrine ephemeral saline |
| Caiquen | 59, 60 | 4.66 | Mesic upland ephemeral |
| Guanaco | 75 | 4.59 | Mesic lacustrine |
| Huesos | 185A, B | 3.00 | Mesic lacustrine |
| Loica | 24 | 4.65 | Mesic lacustrine juncus marsh |
| Puma | 39 | 1.95 | Mesic riverine |
| Roca | 54 | 4.38 | Mesic upland ephemeral |
| STMV | | | |
| Booboo | 88 | 0.22 | Xeric upland |
| Calafate | 93 | 0.17 | Mesic lacustrine |
| Earthwatch | 267 | 2.26 | Mesic riverine |
| Larga | 205 | 4.16 | Xeric upland ephemeral |
| Mellizas | 293 | 0.83 | Mesic riverine |
| Pato Rana | 22 | 5.14 | Mesic lacustrine juncus marsh |
| Peso | 228 | 0.36 | Mesic upland ephemeral |

Table 2. Proportion of time during which FGs were observed on study vegas, n = number of biweekly census periods

| Vega | Proportion |
|---|---|
| FGTM Vegas | |
| Roca | 1.00 |
| Caiquen | 0.94 |
| Blanca | 0.88 |
| Huesos | 0.78 |
| Guanaco | 0.75 |
| Puma | 0.63 |
| Loica | 0.50 |
| n = 7 | $\bar{x}$ = 0.78 ± 0.025 |
| STM Vegas | |
| Larga | 0.38 |
| Pato Rana | 0.33 |
| Peso | 0.25 |
| Calafate | 0.19 |
| Booboo | 0.13 |
| Mellizas | 0.00 |
| Earthwatch | 0.00 |
| n = 7 | $\bar{x}$ = 0.18 ± 0.021 |

portion of a study vega, the remainder of which was dominated by a FGTM. However, portions of vegas held by STM or, presumably, sub-dominant FGTMs were small ($\bar{x}$ = 0.60 ha) in comparison to mean vega area defended by FGTMs ($\bar{x}$ = 1.93 ha)($t = 3.31$, d.f. = 19, $p < 0.01$). Some females used STM vegas in November and December, though the overall number was small ($\bar{x}$ = 2) (Fig. 3). Density of animals with respect to vega area did not differ significantly between FGTM ($\bar{x}$ = 4.6 animals/ha) and STM ($\bar{x}$ = 5.6 animals/ha) vegas during any month ($P \geq 0.1$).

## Forage Characteristics

### Species composition

Treatment means for percent of absolute cover of the 6 most prevalent vega species, based on frequency of occurrence, are presented in Table 3. Although the 6 plant species measured represented 48% (relative occurrence) of all species recorded over all vegas, they occurred in clumps or as dense, mat-like lawns composing from 70-90% (absolute occurrence) of the species in any particular vega. No significant differences were observed between FGTM and STM vegas for any of the species examined. Further analysis of species composition was done because of large, but not significant differences and low sample sizes.

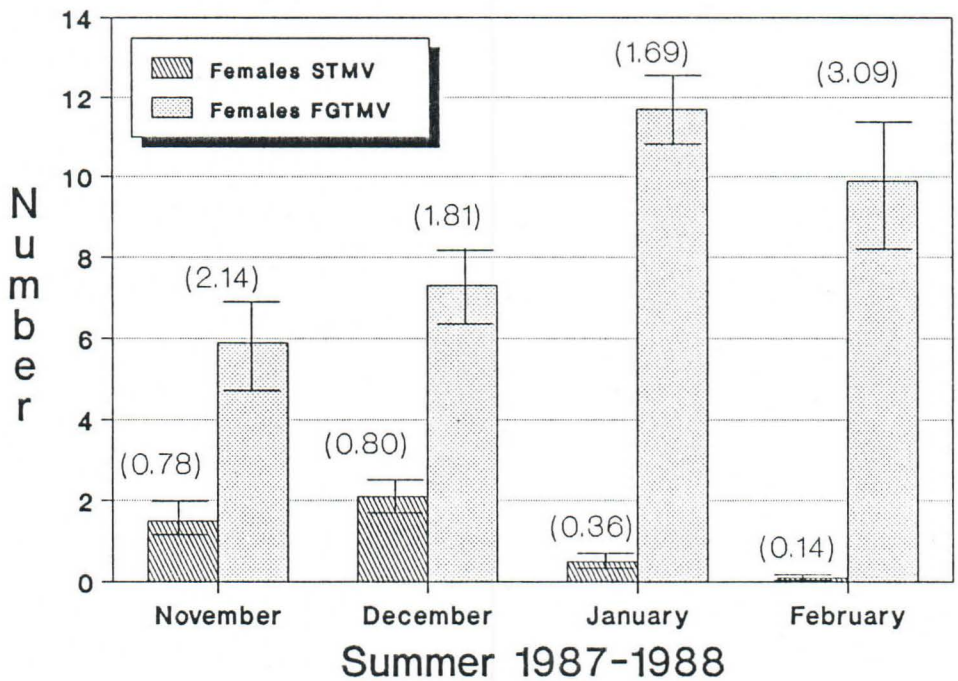


Figure 3. Mean numbers of females observed on 7 FGTM and 7 STM vegas during 7 biweekly census periods from November 1987 to February 1988 in Torres del Paine National Park, Chile

Table 3. Species composition and standard errors of dominant species based on absolute frequency of occurrence in 185 .1-m² loops located in 7 FGTM and 7 STM vegas in Torres del Paine National Park, Chile

| Species | FGTM* | STM* |
|---|---|---|
| Eleocharis pachycarpa | 0.60 ± 0.10 | 0.40 ± 0.10 |
| Carex gayana | 0.48 ± 0.11 | 0.30 ± 0.08 |
| Holcus lanatus | 0.37 ± 0.08 | 0.28 ± 0.07 |
| Agrostis capillaris | 0.29 ± 0.08 | 0.46 ± 0.08 |
| Hordeum comosum | 0.23 ± 0.05 | 0.23 ± 0.09 |
| Potentilla anserina | 0.20 ± 0.08 | 0.37 ± 0.08 |

*Species means did not differ significantly between vega types ($P > .10$).

Mean totals of number of females and all animals observed per vega were regressed on each of the 6 plant species' percent (absolute) occurrence for each vega. Only presence of Eleocharis pachycarpa was significantly related to mean number of females ($F = 3.30$, $P < 0.10$, $r = 0.46$).

Forage quality

Percent forage moisture content was determined for caged vegetation. Percent and standing CP and DDM, along with proportion of flowering (mature) plants were determined for uncaged vegetation (Table 4).

Moisture content of plants was significantly higher in FGTM vegas than in STM vegas. No significant differences in percent CP or percent DDM were observed between FGTM and STM vegas. Marginally significant differences in unit standing DDM occurred between FGTM and STM vegas, although both unit and total standing CP and total standing DDM values were similar (Table 4). Percent DDM was significantly higher in FGTM vegas than STM vegas in February ($t = 2.40$, d.f. = 12, $P < 0.04$)(Figure 4).

Further analysis of February data showed no relationship between total number of females or of all animals using a vega and percent digestibility. However, higher percent digestibility was positively correlated with the number of territorial males observed occupying

Table 4. Forage quality means and standard errors of habitat in 7 family group territorial male (FGTM) and 7 solo territorial male (STM) vegas during summer 1987-1988 in Torres del Paine, Chile

| Variable | FGTM | STM | P[a] |
|---|---|---|---|
| Percent Moisture | 67.92 ± 0.52 | 60.25 ± 1.01 | 0.01 |
| Percent CP Combined | 10.86 ± 0.41 | 11.03 ± 0.66 | 0.80 |
| Unit Standing CP ($g/m^2$) | 5.5 ±1.2 | 11.0 ± 3.3 | 0.16 |
| Total Standing CP (kg) | 219.8 ± 52.0 | 149.8 ± 57.0 | 0.40 |
| Percent DDM Combined | 46.81 ± 0.78 | 47.28 ± 1.10 | 0.75 |
| Unit Standing DDM ($g/m^2$) | 19.0 ± 4.4 | 41.7 ±10.2 | 0.07 |
| Total Standing DDM (kg) | 726.8 ±182.6 | 742.4 ±332.0 | 0.98 |
| Proportion of Flowering Plants | 0.18 ± 0.36 | 0.28 ± 0.53 | 0.05 |

[a]Probability of a greater t-statistic.

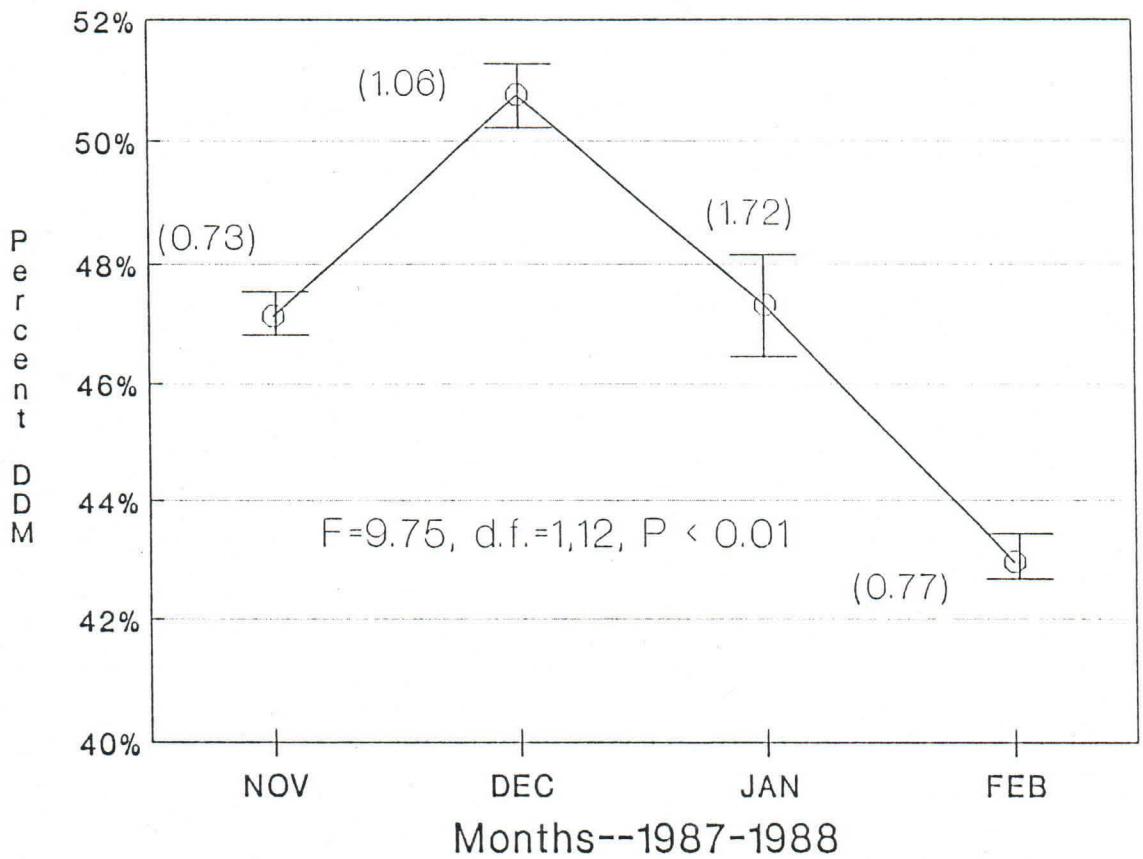


Figure 4. Mean percent digestible dry matter (DDM) of forages on 7 FGTM and 7 STM vegas from November 1987 to February 1988 in Torres del Paine National Park, Chile. The F statistic represents the overall linear relationship of all FGTM and STM vegas combined

a vega site ($F = 7.08$, $P < 0.03$, $r = 0.61$).

A significant time effect was noted for all variables collected as repeated measures. Percent DDM ($F = 9.75$, $P < 0.01$) and CP ($F = 23.09$, $P < 0.001$) decreased significantly in both FGTM and STM vegas (Figs. 4 and 5, respectively). A significant monthly trend could not be established for either total or unit CP and DDM ($P > 0.10$). However, gross examination of CP and DDM trends indicate that changes between November and December paralleled relationships observed in percent CP and DDM analysis previously discussed.

The proportion of flowering plants was significantly lower in FGTM vegas than in STM vegas (Table 4). A significant time ($F = 56.0$, $P < 0.001$) and a time by vega type interaction ($F = 4.76$, $P < 0.02$) for proportion of flowering plants were observed (Fig. 6).

Forage quantity: caged vegetation

Coefficients of variability (CV) were calculated for each vega based upon pre-study clippings of sites near cages, and post-study clippings of caged sites. Pre-study clipping CVs ranged from 47 to 138 in STM vegas and from 0 (no measurable vegetation) to 109 in FGTM vegas. Final clipping CVs ranged from 13 to 72 in STM vegas and from 17 to 77 in FGTM vegas. Based on coefficient of variability

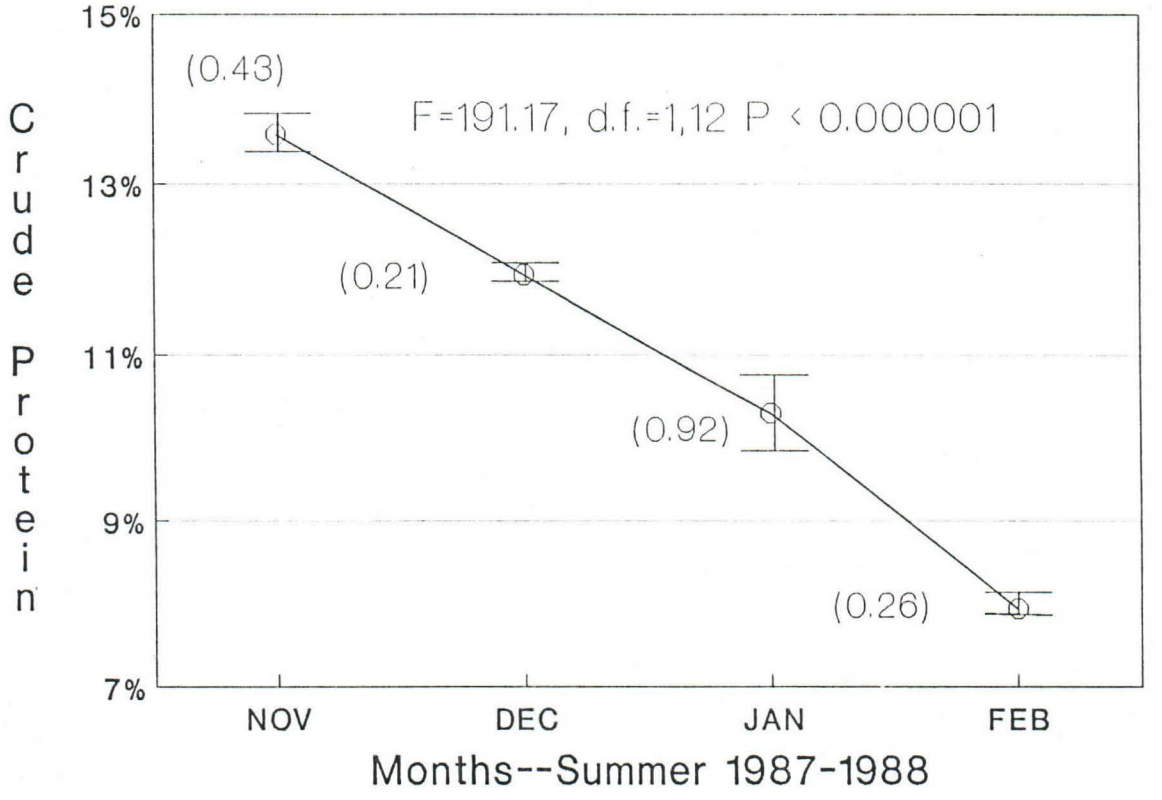


Figure 5. Mean crude protein of forages on 7 FGTM and 7 STM vegas from November 1987 to February 1988 in Torres del Paine National Park, Chile. The F statistic represents the linear relationship for all STM and FGTM vegas combined.

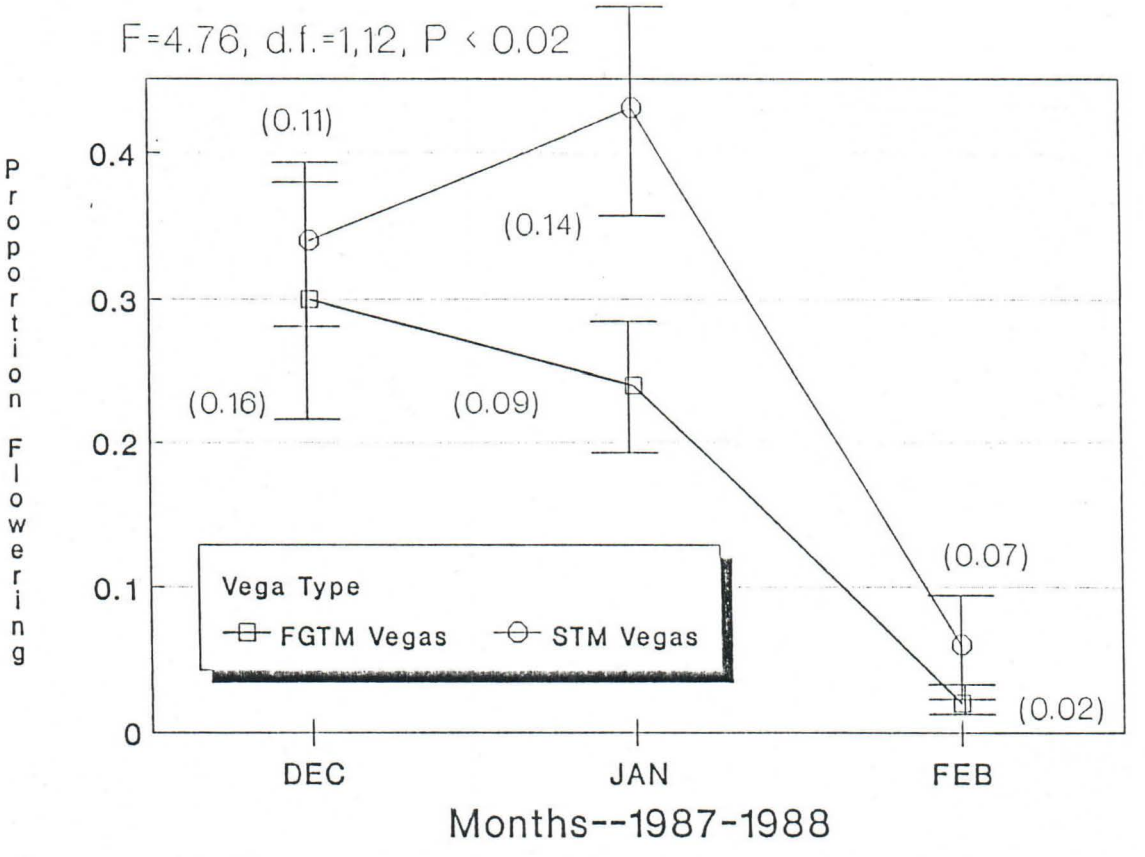


Figure 6. Mean proportion of plants flowering on 7 FGTM and 7 STM vegas from November 1987 to February 1988 in Torres del Paine National Park, Chile. The F statistic represents the vega type x time interaction

results, 5 vegetation cages located in each vega were deemed adequate for sampling standing crop and productivity measurements.

Productivity on a per unit basis was greater in STM vegas than in FGTM vegas (Table 5). No significant differences between FGTM and STM vegas were observed in total productivity. An analysis of covariance on total productivity data was done to increase precision of detecting treatment differences by using initial clipped vegetation weights as covariates. But no significant difference between FGTM and STM vegas was observed ($F = 2.5$, $P = 0.14$).

Forage quantity: uncaged vegetation

The proportion of grazed plants was higher in FGTM vegas than in STM vegas (Table 5). Grazing pressure increased significantly over time, based on proportion of plants grazed ($F = 21.77$, d.f. = 1, 12, $P < 0.001$)(Fig. 7). However, the monthly trend was dependent upon the type of vega being observed ($F = 8.09$, d.f. = 1, 12, $P < 0.02$). STM vegas sustained lower levels of grazing between December and January than did FGTM vegas. Grazing increased on STM vegas from December until February, though still at a substantially lower level and rate than on FGTM vegas (Fig. 7).

Table 5. Productivity, availability, utilization means and standard errors of caged and uncaged vegetation in 7 family group territorial male (FGTM) and 7 solo territorial male (STM) vegas in Torres del Paine National Park, Chile

| Variable | FGTM | STM | P[a] |
|---|---|---|---|
| CAGED VEGETATION: | | | |
| Per Unit Productivity (Standing crop g/m²) | 1980 ± 211 | 3230 ±324 | 0.01 |
| Vega Total Productivity (Total Standing crop in kg) | 8500 ±1100 | 6619 ±2857 | 0.55 |
| UNCAGED VEGETATION: | | | |
| Per Unit Standing Crop (Standing crop g/m² under grazing) | 42 ±10 | 86 ±20 | 0.08 |
| Vega Total Standing Crop (Total Standing crop under grazing in kg) | 1666 ±424 | 1532 ±673 | 0.98 |
| Forage Availability (Plant Height in cm) | 8 ±2 | 16 ± 2 | 0.14 |
| Total Forage Availability Index (Plant Height*Area) | 35 ± 8 | 37 ±11 | 0.58 |
| Proportion of Grazed Plants | 0.4 ±0.06 | 0.1 ±0.02 | 0.001 |

[a]Probability of a greater t-statistic.

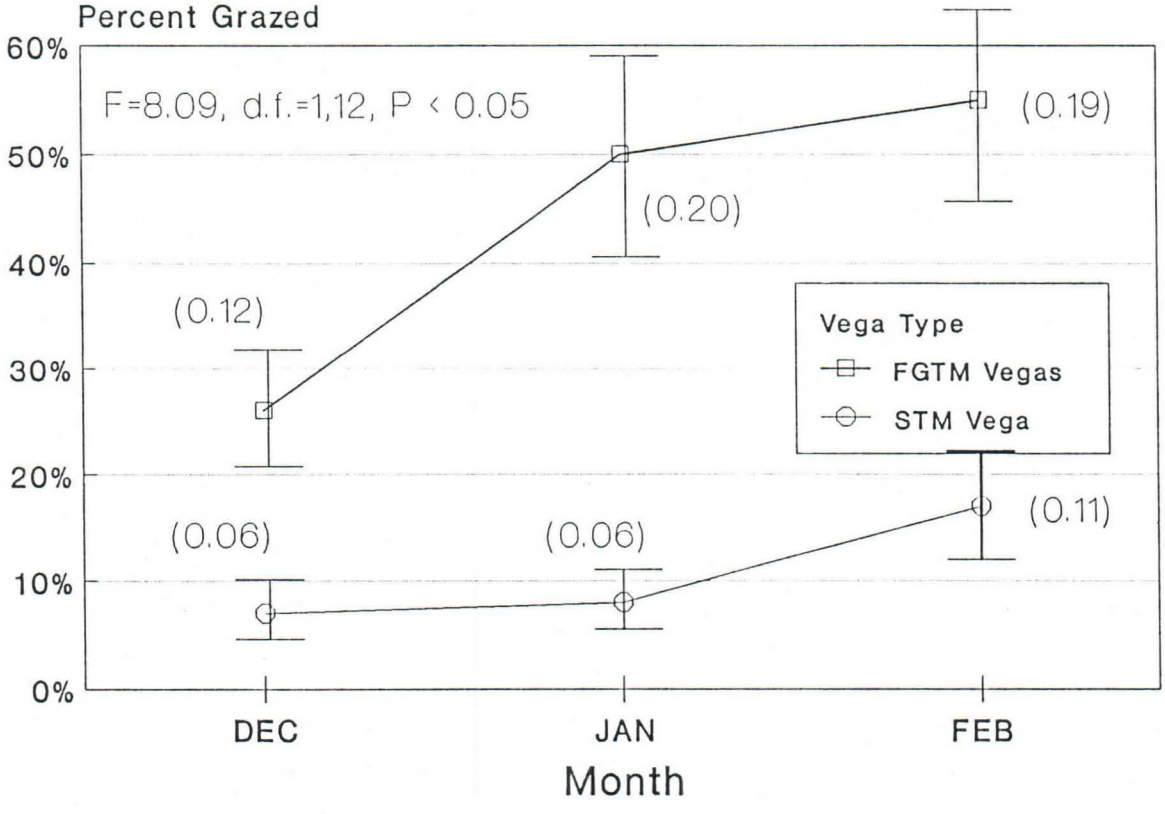


Figure 7. Mean proportion of plants grazed on 7 FGTM and 7 STM vegas from November 1987 to February 1988 in Torres del Paine National Park, Chile

FGTM vegas had only marginally lower unit standing crop under potential grazing than STM vegas (Table 5). Total vega standing crop under potential grazing did not differ significantly between vega types. Neither total nor unit standing crops changed appreciably between November and December ($P > 0.10$). Neither indices of unit nor total forage availability differed between FGTM and STM vegas (Table 5).

An analysis was conducted to determine whether forage availability, maturity, or grazing use in the previous month (month n-1) was related to vega use in the current month (month n). A significant relationship was determined between number of females and proportion of plants grazed during the previous month ($F = 28.89$, d.f. = 1,12, $P < .001$, $r = 0.64$) (Fig. 8). Inclusion of a quadratic term did not increase $r^2$ appreciably. Previous month's availability and maturity were not significantly related to vega use the following month ($P > 0.10$).

From forage characteristic analyses, variables that appeared to influence female selection and use of vega habitat (and their relationship) were vega use during the previous month (+), forage moisture content (+), unit productivity (-), plant maturity (-), unit standing DDM (-), unit standing crop under grazing (-). Percent occurrence of ELPA was positively related to number of

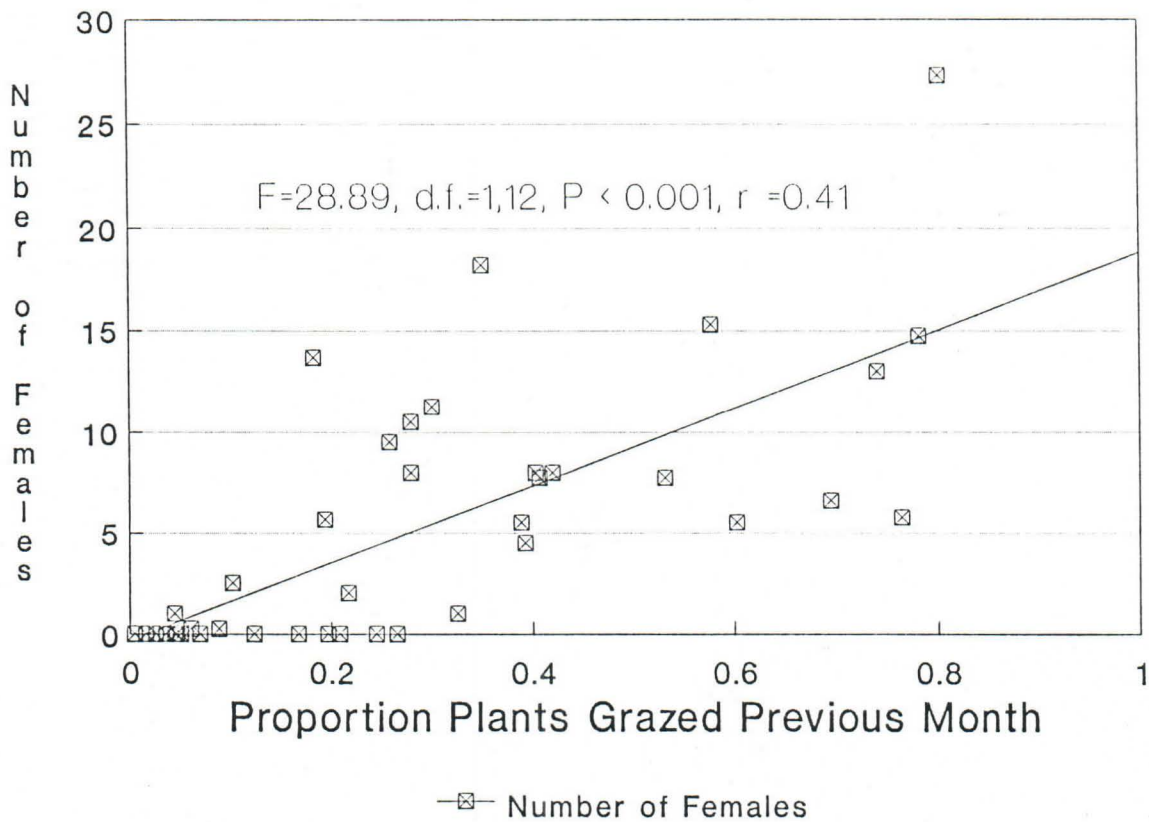


Figure 8. Proportion of plants grazed during the previous month and female use of 14 study vegas in Torres del Paine National Park, Chile

females using vegas, but was not indicative of female selection of vega habitat based upon FGTM/STM vega comparisons.

## Physical Characteristics

### Reanalysis of predation data

A reanalysis of data from Iriarte's (1988) study of puma in TPNP was conducted to extract information about puma predation of guanacos on vega areas. Of 85 total guanaco mortalities directly attributed to pumas, 35 (41%) occurred on a vega and 9 (11%) occurred within 25m of a vega. Thus, 52% of all guanacos killed by pumas were associated with vegas. Moreover, 85% of all possible puma kill-sites were located near bottoms of depressions and ravines. Even though these kill sites could not be associated directly with vegas due to the nature of the data, such locations are likely sites for patches of vega vegetation.

### Vega area and perimeter

Vega total area and total perimeter differed significantly between FGTM and STM vegas (Table 6). FGTM vegas had approximately double the area and perimeter of STM vegas.

Peripheral cover and slope

PCI (peripheral cover index) was 7.5 times higher for STM vegas than for FGTM vegas (Table 6). As expected, absolute peripheral cover did not differ significantly between FGTM and STM vegas (Table 6). However, there were marginally more areas of peripheral slope on FGTM than on STM vegas (Table 6). Percent peripheral cover, percent peripheral slope, and PSI did not differ significantly between the two vega types.

## Correlation Analysis

A summary of correlation analysis is given in Table 7. An importance rank was assigned to each variable based upon the strength of its relationship with female days of vega use (FDU). Proportion of plants grazed in the previous month was most strongly correlated with FDU, indicating either animal response to resource enhancement under grazing or tradition. Area and perimeter, both highly intercorrelated ($r = 0.61$, $P < 0.03$), were second most strongly correlated with FDU, indicating female use, and probably preference, of open areas. Moisture content, unit productivity, slope, and PCI risk index were third most strongly correlated with FDU. Unit standing DDM, plant maturity, and occurrence of ELPA were fourth, fifth, and sixth most strongly related to FDU.

Table 6. Means and standard errors of physical characteristics of habitat in 7 FGTM and 7 STM vegas in Torres del Paine National Park, Chile

| Variable | FGTM | STM | P[a] |
|---|---|---|---|
| Surface Area (ha) | 4.5 ±0.8 | 1.9 ±0.8 | 0.03 |
| Perimeter (m) | 1330 ± 135 | 600 ±175 | 0.01 |
| Peripheral Cover (m) | 680 ±109 | 440 ±146 | 0.19 |
| Peripheral Slope (m) | 440 ± 75 | 230 ± 96 | 0.10 |
| % Periph. Cover | 51 ± 6 | 66 ± 13 | 0.29 |
| % Periph. Slope | 33 ± 3 | 30 ± 7 | 0.76 |
| PCI[b] | 1.23 ±0.34 | 9.22 ±4.15 | 0.10 |
| PSI[b] | 0.74 ±0.15 | 4.57 ±2.56 | 0.19 |

[a]Probability of a greater t-statistic.

[b]PCI = Percent peripheral cover per unit area; PSI = Percent peripheral slope per unit area.

Table 7. Correlation summary of factors and associated variables related to female days of vega use, their relationship (+/-), and probability of a greater test statistic for variables that differed significantly between FGTM and STM vega types

| Factors | Correlation Coefficient | Importance Rank | Probability |
|---|---|---|---|
| **FORAGE CHARACTERISTICS** | | | |
| Quality: | | | |
| % occurrence ELPA | +0.46 | 6 | < 0.10 |
| moisture | +0.54 | 3 | < 0.05 |
| unit standing DDM | -0.53 | 4 | < 0.06 |
| maturity | -0.52 | 5 | < 0.06 |
| Quantity: | | | |
| unit productivity, caged | -0.54 | 3 | < 0.05 |
| unit standing crop, grazed | -0.56 | 2 | < 0.04 |
| grazing use previous month | +0.87 | 1 | < 0.001 |
| **PHYSICAL CHARACTERISTICS** | | | |
| surface area | +0.76 | 1 | < 0.002 |
| perimeter | +0.78 | 1 | < 0.04 |
| peripheral slope | +0.54 | 3 | < 0.05 |
| peripheral cover index | -0.54 | 3 | < 0.05 |

# DISCUSSION

## Vega Utilization and Guanaco Group Size

Vega plant communities are a key component in guanaco habitat at TPNP and are especially important to FGs. Of all animal observations on vegas (1980), 72% involved FGs. Traditional (1-3 years prior) vega use by FGs and SMs was a reliable predictor of FGTM or STM use of vegas during following seasons. However, FG use (whether or not a family group used the site in the past) and future FG size may not necessarily be related. Family group size at any given instant probably cannot be predicted solely on the basis of previous FG use except in the sense that FG use will imply a group size greater than 1. For example, daily FG sizes on vegas are variable. I have observed 4 females within a male's territory during one day, and over 40 the next. Given such variability, precise group size prediction from use data is much less possible than prediction of family group use. Nevertheless, our data do strongly indicate that average FG size may be a good potential predictor of the average size of FGs that will use the site in the future.

Female use of "STM" vegas in December may indicate a shifting of females among territories during the breeding season. Increased social interactions and aggressive

approaches by territorial males may force some females off FGTM territories at this time. Higher rates of aggressive encounters involving territorial males in December have been reported (Jurgensen 1985). Alternatively, a small proportion of females may be using STM vegas to avoid feeding competition experienced in larger groups using FGTM vegas, or some females may have bred early in the season or not at all and thus found no advantage to remaining in FGs.

## Forage Characteristics

Simple and direct foraging relationships between ungulate selection of habitat and forage production, availability, and foraging efficiency have been demonstrated in a variety of ungulates (Irwin and Peek 1983, Takatsuki 1983, Hanley 1982, Canon et al. 1987). More commonly, however, forage quality and quantity affect habitat selection by ungulates in complex and interactive ways.

### Species composition

Percent occurrence of ELPA was 1.5 times greater in FGTM vegas than in STM vegas (Table 3). Though this difference was only marginal, significantly more animals were observed on vegas with higher percent occurrence of

ELPA, suggesting guanaco selection for vegas containing large amounts of ELPA (Table 7).

ELPA was the most common plant encountered on both FGTM and STM vegas. This finding contrasted with earlier data, which identified Holcus lanatus as the most common vega species (Ortega and Franklin 1988). Differences in methodology, and not botanical changes, were suspected to account for apparent differences.

Guanacos may be selecting for some qualitative aspect associated with ELPA, assuming that ELPA is an important food source for guanacos. Although quantitative data indicating guanaco foraging of ELPA is lacking, I have observed 1) guanacos feeding on ELPA dominated mats of vega vegetation, 2) highly cropped mats of ELPA in the same vegas that apparently received only guanaco use, and 3) fragments of ELPA in microhistological slides of guanaco feces.

Like some other members of the sedge family, ELPA grows as short, cylindrical, succulent shoots that form a dense, mat-like lower layer in moist vegas or dense patches in drier vegas. Moisture content of ELPA on vegas during 1987-88 was as high as 60%. Occurrence of ELPA was correlated ($r = .53$ $p < .01$) with percent moisture of vega vegetation. Percent moisture differed significantly between FGTM and STM vegas, further indicating potential guanaco selection for moisture rich vegetation under arid conditions.

Guanacos are non-obligate drinkers and supply most of their water needs via their diet (Franklin 1982). Impala, a non-obligate drinker, must drink free water when forage moisture contents drop below 30% (Jarman and Sinclair 1979). Elk and deer in North America also have shown high preferences for nutritionally valuable (and moisture-rich) meadow vegetation (Harper et al. 1967, Swanson 1970, Kufeld 1973, Collins and Urness 1983).

We observed more guanacos drinking from free water sources during summer 1987-88 than in previous years, again implying the possibility of moisture stress on guanacos, and thus supporting the hypothesis of selection for forages with high moisture content. The Chilean Patagonia is a normally arid region and in 1987-88, experienced a drier than normal summer (TPNP Weather Records 1970-1988, J. Gonzalez, CONAF, Puerto Natales, Chile, pers. comm.). ELPA may maintain moisture content during arid conditions because it is typically found growing on lowland sites low in the vegetation canopy under mesic conditions.

A concurrent hypothesis is that ELPA, and other densely-growing forages provide a concentrated, high quality resource for grazing guanacos. Such a resource would supply guanacos with a means of potentially increasing foraging efficiency because animals would have to move less in areas of concentrated forage availability (Pyke 1984). Burned

areas in Utah were preferred by elk, not because of nutritional differences of post-burn vegetation, but rather due to increased foraging efficiency associated with the high predictability with which preferred species occurred (Canon et al. 1987).

Additionally, location of free water has been identified as an important factor, especially to lactating females, in ungulate habitat selection (Miller 1974, Marcum 1975, Nelson and Burnell 1975, Thomas et al. 1976, Bryant and Morrison 1985). Reliance upon free water in TPNP may be risky because it involves more activity and greater chance of detection by predators as animals move to and concentrate at watering locations. Guanacos observed in this study had essentially equal access to free water because all study vegas occurred within 1 km of free water, and many had water on site. Many lakes, ponds, and watercourses in the study area, however, are associated with rocky, steep slopes and are frequented by the Patagonia puma (Wilson 1984, Iriarte 1989). Avoidance of or reduction in free water use in potentially dangerous habitats would be adaptive for decreasing predation risks as long as water needs could be met through the availability of moist forages.

Qualitative evidence for increased predation risks associated with free water or visual obstruction cover has been observed by researchers at TPNP over the past several

years. Guanacos that are occasionally observed using watering areas in which there is puma activity and peripheral cover are more vigilant in their anti-predator behavior (W. Johnson, Dept. of Animal Ecology, Iowa State University, Ames, Iowa, pers. comm., A. Iriarte, Dept. of Animal Ecology, Iowa State University, Ames, Iowa, pers. comm.). Shores of Lake Sarmiento are, based on telemetry observations, highly frequented by pumas. Here it is difficult for us to approach to within 1 km without disturbing/dispersing guanaco FGs, while in other areas of the peninsula, we have approached FGs as close as 0.05 km without alarming or dispersing group members. Underwood (1982) and Berger et al. (1983), presented evidence that African antelopes and North American pronghorn modified their foraging behaviors and increased their visual vigilance in areas of greater predation risk.

Forage quality

Moisture content of meadow vegetation, as discussed, was important in guanaco site selection. Other indices of forage quality among vegas were fairly uniform despite differences in unit standing DDM between FGTM and STM vegas. This was primarily because FGs used larger vegas with lower unit productivities and SMs used smaller vegas with higher productivities. Although unit DDM was higher on areas not

used by females, this was probably a function of higher standing crops (for both caged and uncaged vegetation) on STM vegas (Table 5).

A marginally significant increase in number of females with increased unit DDM was observed in December. Females may be selecting for higher forage digestibility during December, a period marked by falling forage CP levels and increased nutritional demands of heavy lactation and breeding (Jurgensen 1985). Jurgensen (1985) also showed that female use of vegas increased as water levels receded in December, and thus exposed additional immature, (highly digestible) moisture and nutrient rich vega vegetation.

Apparently, most FG guanacos were not selecting vegas on the basis of total protein and digestible dry matter production. Only during February, at the end of the growing season and when females were found in greater numbers on FGTM than STM vegas, was forage significantly more digestible in FGTM than STM vegas (Fig. 4). Animal selection for forage quantity and quality may have become important in maintaining high nutrition as the growing season waned and available forages decreased in quantity and quality due to grazing and senescence. Late summer is an important nutritional period when females are suckling young and preparing for winter, but when plant protein levels are low. Also, annual east to west guanaco migrations at TPNP

may be associated with higher availability of quality, cured forages in winter-range vegas that remained little-used during summer (Ortega and Franklin 1988).

Previously discussed total CP and DDM analysis suggested no quality differences between vega types. However, FGTM vegas contained less flowering vegetation than STM vegas, indicating that they contained more immature forages of higher quality than rank, mature forages associated with STM vegas. Plant maturity, in terms of proportion of flowering vega plants, is an index of plant quality, assuming that forage quality decreases with the physiological processes involved in maturity, anthesis, and senescence (Van Soest 1982). Moisture content was also significantly higher on FGTM vegas than STM vegas. Moisture content coincides with varying protein and other nutritional characteristics in forages and also decreases with continuing plant maturity (Van Soest 1982). This suggests that quality of FGTM vegas actually may have been retained at higher levels than STM vegas. Additionally, rates of decline for DDM, though statistically similar between FGTM and STM vegas, suggest longer retention of forage quality by FGTM than STM vegas (Fig. 4).

Although differences in measures of CP and DDM were not relatively apparent between FGTM and STM vegas, changes in forage quality during the summer were grossly associated

with female use of vegas. Percent DDM for both FGTM and STM vegas peaked in December and gradually decreased thereafter, while CP decreased consistently over the duration of the study (Figs. 4 and 5). Female use of vegas likewise rose through December into January, but fell thereafter (Fig. 3).

Prolonged quality in FGTM as opposed to STM vegas was suggested by a vega type and time interaction for both proportions of flowering and grazed plants and may be indicative of the "grazing lawn" effect (McNaughton 1984). "Grazing lawns," are areas of vegetation maintained in an immature, vegetative, and potentially more nutritious state due primarily to grazing influences (McNaughton 1984, 1985, 1986). Forages in FGTM vegas may have been retained in a vegetative, potentially more nutritious stage by intense grazing by FGs (Figs. 6 and 7). Areas that contained more immature forages, such as FGTM vegas, received higher female use (Fig. 3) and, as a result, more grazing than areas of vegetation that had matured (STM vegas)(Fig. 7). Our results indicated that more females used areas that had sustained greater grazing pressure during the previous month, or in other words, vegas that received high use during the previous month continued to receive high use during the current month in spite of lower unit productivity on FGTM vegas (Figs. 7 and 8). That female, and thus FG use of heavily grazed vegas that posessed immature forages

remained high and actually increased throughout the study was further evidence of the grazing lawn phenomenon.

Alternately, female selection of grazed vegas could be simply a product of habit or tradition. Year to year use of vegas is predictable, indicating that vega use by females from month to month may also be tradition related. This hypothesis is especially strong if group size remained constant from day to day, and if the same individuals used vegas that they had previously inhabited the year before. However, our data indicate that group sizes were variable from day to day, and actually increased during the summer. Moreover, the same females did not always stay on the same vegas, a common guanaco trait (Franklin 1983, W. L. Franklin, Dept. of Animal Ecology, Iowa State University, Ames, Iowa, pers. comm., K. Harms, Dept. of Animal Ecology, Iowa State University, Ames, Iowa, pers. comm.). Although it is important in predicting FG use of vegas, tradition does not totally explain variation in either selection or group size.

Forage quantity

Caged vegetation protected from grazing (unit standing crop) was 1.6 times higher in STM than in FGTM vegas. Total standing crop of caged and grazed vegetation in FGTM and STM vegas did not differ significantly. Similarity of standing

crops in FGTM and STM vegas suggests similar absolute productivity of FGTM and STM vegas despite the fact that FGTM vegas are more than 2 times larger than STM vegas. STM vegas may produce more forage on a per unit basis because smaller vegas frequently occur under mesic conditions where water supplies to vegetation may be relatively more concentrated than on larger, more open, more exposed FGTM vegas.

Grazed standing crop similarity between the two vega types may be a result of small, highly productive STM vegas receiving relatively little use, while less productive (on a unit basis), but larger FGTM vegas received higher use, perhaps stimulating productivity. Under some conditions, grazing can stimulate productivity (Vickery 1972, Adjei et al. 1980, Owen 1980, McNaughton 1983, Olson and Richards 1988). Caged (non-grazed) unit standing crops were greater on STM vegas, but uncaged unit standing crops were similar between FGTM and STM vegas. Uncaged vegetation should have been much reduced in FGTM vegas that were under more intense grazing pressure than SM occupied vegas. Our data also suggested that total forage productivity and availability were relatively constant among FGTM and STM vegas, regardless of whether they were calculated using caged or uncaged treatment values. This result also supports the stimulated productivity hypothesis. FGTM vegas with their

much higher use intuitively should have showed lowered total availability and productivity under grazing. These results provide some evidence that grass production in FGTM vegas may have exceeded that of STM vegas. This hypothesis was not rigorously tested, however, because continuous clipping of exclosures to simulate grazing was not feasible.

## Physical Characteristics

### Puma predation

Pumas and their historic use of guanaco populations are suspected to have influenced guanaco habitat use during this study. Predation by the Patagonia puma is a significant cause of guanaco mortality at TPNP. Puma densities in TPNP are reported among the highest of any populations studied (Iriarte et al. ms in preparation). Probable puma kills, determined from examination of guanaco skulls collected from 1979-1988 accounted for one-third of all guanaco mortality in TPNP (Iriarte 1988).

Guanacos, through selection of "safe" habitats, may be responding and adapting in order to minimize predation risks. Topography and other habitat physical features may be used by pumas during their search for prey (Wilson 1984, Cajal and Lopez 1987). Analysis of 45 kill-sites indicated that shrub cover (22%) was 3 times higher near kill-sites

than covers reported for the peninsula as a whole (Wilson 1984, Iriarte 1988). Additionally, 85% of all kill-sites were found at the edge of trails located in or leading from bottoms of depressions or ravines (Iriarte 1988). Pumas typically must stalk their prey and rely upon stealth and secrecy in order to approach close enough for a successful kill. Pumas probably attack their prey most frequently from elevated, hidden positions (Wilson 1984, Hornocker 1970b). Vega habitat was associated with 52% of puma-killed guanacos, and therefore is an important site in investigating and understanding puma-guanaco predator-prey relationships.

Vega area and perimeter

Family groups used vegas that were larger, with greater amounts of periphery, than vegas used by STMs. Vega perimeter, which was correlated with area, was considered mainly a function of vega area. Its relation to female use, then, could be included as a component of vega surface area without giving it separate consideration. Surprisingly, larger FGTM vegas accounted for similar overall standing crops compared to STM vegas. The forage productivity aspect of area did not explain selection or group size. Therefore, some other aspect of "area" and perimeter influenced female selection and group size.

Females could have selected larger sites because of the "appearance" of a group, generated by more than one territorial male typically occupying larger vegas. Females may be attracted to vega resources. However, data from this study have shown that although occurrence of ELPA and other dynamics of forage quality may differ among the two vega types, STM and FGTM vegas are similar with respect to many resource aspects. Forage related factors do not adequately explain vega site selection or FG size.

A plausible explanation is that females may use area, or rather, the existence of open space, as "cover." Vicuna and guanaco in San Guillermo reserve, Argentina selected open, flat areas of gentle slope as opposed to steeper, rocky slopes (Cajal 1989). Cajal and Lopez (1987) indicated that pumas may use rocky slopes in stalking and killing guanacos in San Guillermo. North American pronghorn (Antilocapra americana), an animal that also evolved in North America and that shares a remarkably similar social system with the guanaco (Franklin 1983), has demonstrated the ability to use open space as a defense against predators (Kitchen 1974). Escape cover, including open space, commonly influences habitat use and foraging relationships of other ungulates that are preyed upon by puma as well (Collins and Urness 1983, Stuewe and Hendrichs 1984, Risenhoover and Bailey 1985, Lagory 1986).

Peripheral cover and slope

PCI was used as an index of predation risk to an animal owing to a combination of the relative amount of vertical cover that obstructs vision, and animal proximity to that cover. FGTM vegas had appreciably lower PCI values than STM vegas, and FGTM vegas were used significantly more than STM vegas by females. PCI differences between FGTM and STM vegas were only marginally significant, probably a function of small sample size. Females selected open spaces with lower amounts (relative) of peripheral obstruction cover. Female guanacos may have selected habitats, at least in part, on the basis of less risk to predation owing to visual obstruction cover. Vegas were selected that had either little visual obstruction cover present, or, if peripheral cover existed, it was effectively "removed" from proximity with grazing animals because of large vega area and openness.

Although it approached significance, peripheral slope was not considered a possible contributing factor in explaining group size because it was positively correlated ($r = 0.88$, $P < 0.001$) with area and periphery. In other words, larger vegas with more perimeter had greater chances of including areas of higher peripheral slope.

Previously discussed observations of increased vigilance in guanaco groups that occasionally used smaller

vegas, or vegas with high peripheral cover provide further evidence that guanacos in such situations are "at risk" to predation. Increased vigilance and other behaviors that mediate predation risk may occur in response to visual obstructions in the environment (Risenhoover and Bailey 1985, Lagory 1986). Further, data from previous studies suggest that more guanacos were killed by pumas on the winter range than on summer range (Wilson 1984, Iriarte 1988). Winter range vegas were typically accompanied by higher amounts of peripheral cover, and smaller total areas than vegas on summer range (Wilson 1984). Although guanaco use of vegas during harsh winters may be low due to snow cover of vega vegetation (Ortega and Franklin 1988), a high degree of winter vega use has been documented (W. Johnson and W. L. Franklin, Dept. of Animal Ecology, Iowa State University, pers. comm.). Reduced use of smaller vegas with high amounts of peripheral cover would, therefore, seem adaptive.

Long-term evolutionary pressures influencing vega selection on the foraging side of the equation should prove stronger than other potential factors because the cost of not foraging is certain death, and the costs of not foraging efficiently are reduced health and vigor. However, costs associated with increased exposure to predation risks may be less immediate than the costs of not foraging, or may even

be outweighed by the payoff. However, evolution could still favor temporary hunger or poor nutrition if they effectively decrease the chance of predation in the case where use of a resource actually places an animal at high risk to predator attack. Simple foraging and predation models indicate that animals can reduce nutritional stress (and chances of starving) by increased foraging or forage searching activity. Even though modifying foraging behavior in these ways could increase an animal's risk to predation, the net result is an optimized mean energy gain and a reduction in overall mortality to other causes (McNamara and Houston 1987).

## Correlation Analysis

Even though most correlations were not high, it is important to remember that "biologically" and "statistically significant" may not always be mutually inclusive terms. Any variable, therefore, that shows logical potential for explaining variation in group size can be helpful in understanding such a complex interaction of events.

That neither forage nor physical characteristics individually dominated results of t-tests (indicating female selection) or correlation analysis (indicating relations with group size) demonstrated the importance of both factors

in understanding habitat use by guanacos in TPNP. Differences in intensities of correlation (correlation coefficients) indicated that prior grazing was most related to female use. To implicate prior grazing use as the major cause of female selection and use of vegas would be problematic because of the nature of this variable. Grazing use simply identified a vega as used and if a vega was used during one month, it was likely to be used the next month. However, vegetation changes that occurred with grazing showed that used vegas may have been more attractive to guanacos than unused ones. For these reasons, grazing use, therefore, was not considered more or less important than any other of the top ranked variables based on correlation analysis.

Vega surface area and perimeter, both highly intercorrelated, were also highly correlated with female use (Table 7). Larger vegas can be less ambiguously related to animal use than can a measure of prior grazing, and reasons for this selection seem clear based upon previous discussion of predation influences. Unit productivity, unit standing crop under grazing, peripheral slope, PCI, forage moisture, and forage maturity were also related to female use. Their intensities of correlation with female use were similar and corroborated evidence of female selection previously discussed. The weakest significant correlation was observed

between occurrence of ELPA and female use (Table 7). It is possible, then, that female use was based upon some other aspect than ELPA, such as moisture content, which was correlated with occurrence of ELPA.

## Conclusions

Previous months' grazing status (a forage characteristic that ultimately affects foraging quality and efficiency), and surface area (a potentially predation related physical characteristic) were the most related to female use and selection of vegas. Dietary/foraging and vega physical characteristics which can be related to predation, therefore, may both act strongly in the TPNP ecosystem in determining vega use and distribution of guanaco FGs (Table 7).

Females may have initially selected vegas on the basis of positive forage characteristics. Selection among vegas, however, was less ambiguously related to surface area, or to other factors that were not measured in this study and that could be associated with surface area, such as behavioral constraints on spacing of individuals (Table 7). Guanaco response to predation-related physical characteristics of vegas may mediate dietary factors that influence habitat

selection, and in this way influence guanaco social organization.

Predation may actually be more important and thus a more detectable factor influencing guanaco response to predation during the relatively forage-abundant summer-territorial period (when this study was done), than it is in winter, when nutritional stresses may come into play (McNamara and Huston 1987, M. Behl, Dept. of Animal Ecology, Iowa State University, pers. comm.). This is because animals may forage on adequate resources in summer and therefore 1) have more time to scan for predators and 2) move around less, thus reducing chances of detection by pumas. Although predation rates increase during winter (Iriarte 1988), this may be because guanacos must forage and move more to maintain a positive or subsistence nutritional balance and therefore do not have the luxury of expending energy to ensure a totally predation-safe existence.

## Recommendations

Predator-prey ecology in TPNP is clearly a complex web of interrelated factors. Future studies of foraging ecology should be conducted to control for factors identified in this study that could potentially influence foraging ecology of guanacos. Only in this way can researchers hope to

isolate and manipulate influences of primary interest. Additional vegetation studies should be conducted using large (10-20$m^2$) grazing exclosures in at least 25 vegas and including clipping (simulated grazing) experiments to see if vegetation in FGTM vegas is producing more vegetation under grazing than STM vega vegetation. Closer spacing of study vegas and automated clipping shears could make this logistically feasible. Weekly or biweekly censuses of vegas and territories is a must for investigating group size for foraging ecology studies. Forage quality samples should be collected directly from vegetation that guanacos graze in order to understand selection of forage quality by the grazer. Additionally, quality samples should be collected as soon as possible after grazing so that post-foraging influences upon quality are minimized.

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# APPENDIX: MICROHISTOLOGICAL PLANT KEY OF COMMON "VEGA" SPECIES OF TORRES DEL PAINE NATIONAL PARK, CHILE

# ABSTRACT

Microhistological plant features were used to prepare a dichotomous key of 61 plant species found in Torres del Paine National Park, Chile. Of the 61, 45 are species associated primarily with the "vega" (meadow) habitat type (Pisano 1977). The remaining 16 appear in close proximity to the vega type, but occur in more xeric upland conditions. Plant species were chosen based upon their abundance and dominance in a vegas, and upon presence in guanaco diets (Raedeke 1980). Diagnostic features are explained and their illustrations are included.

# INTRODUCTION

Microhistological identification of plant fragments is a useful technique in determining diets of herbivores ranging from rodents to cattle (Storr 1960, Flinders and Hansen 1975, Hubbard and Hansen 1976, Pena Neira 1977, Hansen and Clark 1977). Though labor intensive, the technique has the advantage of being applied to a large sample size without sacrificing study animals, which makes this technique especially useful for endangered species or in studies conducted in national parks or refuge situations. Moreover, field collection of samples can be accomplished quickly and efficiently. Researchers have developed techniques that not only help in identifying forage species consumed by herbivores, but may also be used to estimate dietary proportions of plant species on a dry weight basis (Sparks and Malechek 1968). The technique is relatively accurate and repeatable. Potential problems of microhistological sample analysis include differential forage digestibilities and/or fragmentation causing over or underestimation of plants in the diet (Sanders et al. 1980). However, improved methods have been developed to assist researchers in correcting for such problems (Williams 1969, Vavra et al. 1978, Vavra and Holechek 1980, Leslie et al. 1983, Leslie et al. 1984). Future advances in automating

the technique could compensate for time intensive lab procedures associated with microhistological plant identification.

# STUDY AREA

Torres del Paine National Park (TPNP) is located in the Andean precordillera (foothills) of the Chilean (or western) Patagonia (51° 3'S, 72° 55'W). The peninsula-shaped study area is located in the center of the park and is bounded by Lake Nordenskjold on the north, Lake Sarmiento on the south, and Lake Pehoe to the west. The dominant vegetation is described as a xeric pre-andean mattoral or shrub association (Pisano 1974). The vega habitat type (Pisano 1977, Moore 1983, Roig and Faggi 1985) is a mesic to marshy meadow dominated by lush vegetation including grasses, sedges, and low-growing forbs. Though they are one of the least represented vegetation types of the peninsula, vegas are a highly important source of forage for guanaco and other herbivores of TPNP (Jurgensen 1985, Ortega and Franklin 1988, Lawrence 1989).

The objective of this project was to produce an illustrated microhistological key to selected plant species occurring primarily within the meadow habitat vegetation type of Torres del Paine National Park, Chile. This project was done in conjunction with a larger study of guanaco use of vega habitat conducted during summer 1987-1988.

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# METHODS

## Sample collection and identification

Samples of plant species were collected from vegas located in the Lago Sarmiento, Laguna Amarga, and Lago Pehoe sectors of the park (Lawrence 1989). Samples were pressed, matted, and dried. Sr. E. Pisano of the University of Magallanes identified samples according to Moore (1983).

## Sample preparation

Samples of each species were reduced to equal particle sizes by using a Wiley grinding mill at a 1mm setting. Pigments were partially removed from fragments by blending material in a 10% hot chlorine bleach solution and during subsequent treatment with Hertwig's pigment clearing solution. Fragments were mounted on glass microscopic slides using Hoyer's mounting medium (Cavender and Hansen 1970, Hansen et al. 1971).

## Definition of stomata types

**Stomata**, or properly, the stomatal apparatus, is composed of three parts: the stomatal aperture (stomate), **guard cells** which control opening and closing of the aperture, and **subsidiary cells**, which occur in conjunction with or completely surround the guard cells (Esau 1953).

Stomata may be classified into several types based upon the arrangement or shape of cells that surround the stomata. This key uses terms outlined by Metcalf and Chalk (1979).

Actinocytic--surrounded by radially elongated subsidiary cells (Fig. 1e).

Anisocytic--surrounded by three subsidiary cells, one of which is usually smaller than the other two (Fig 1b).

Anomocytic--surrounded by cells not differing from other epidermal cells (Fig. 1c).

Diacytic--enclosed by one or more subsidiary cells whose common walls are at right angles to guard cells (Fig. 1a).

Laterocyclic--paracytic stomata in which the two lateral subsidiary cells surround the guard cells completely (Fig. 1g).

Paracytic--accompanied on either side by one or more subsidiary cells parallel to the long axis of the stomatal pore and guard cells (Fig. 1d).

Parallelocytic--with an alternating complex of three or more C-shaped subsidiary cells of graded sizes parallel to the guard cells (Payne 1970)(Fig.1f).

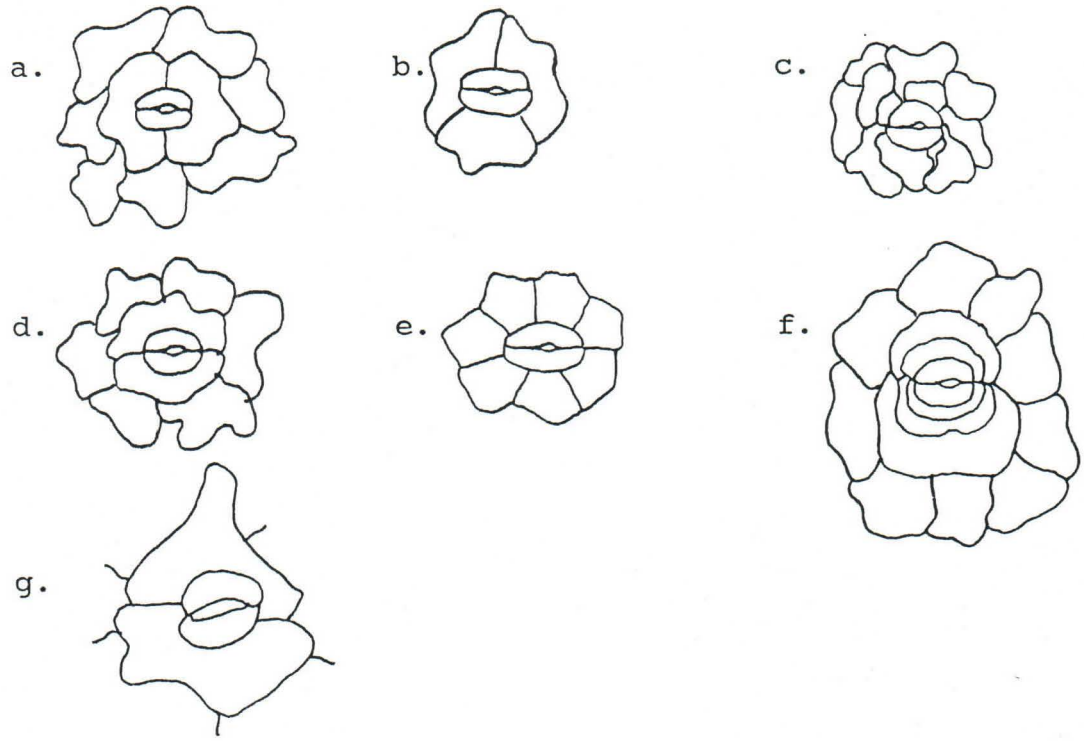



Figure 1. Stomatal guard cell arrangements

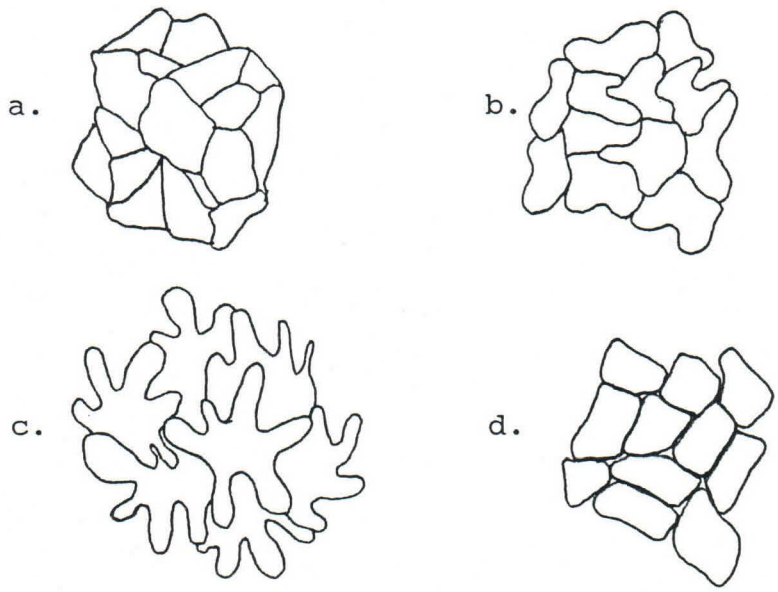



Figure 2. Cell arrangements of forbs and shrubs.
a. angular b. rounded c. jigsaw
d. blocky

Key development

Slides were examined microscopically and diagnostic characteristics were noted. Data were entered into a PC spreadsheet program and sorted according to differing characteristics until individual species were discriminated. Photographs and drawings were made of major characteristics and used as references. Specimens of plants in the key have been donated to the Ada Hayden Herbarium (ISC), Bessey Hall, Iowa State University.

# RESULTS AND DISCUSSION

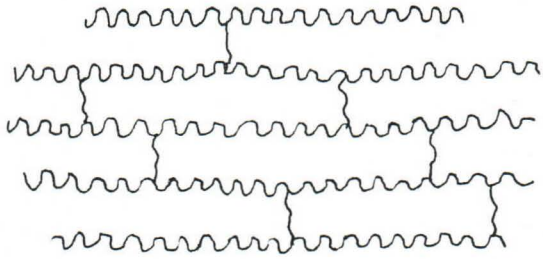
Forty-five common meadow species (species whose percent relative occurrence was greater than 5%) were included in the key (Lawrence 1989). Sixteen additional species that are associated with vegas and that are believed to be grazed by local herbivores were also included in the key. Illustrations of diagnostic characteristics used in identification are included at the conclusion of the key.

## Diagnostic characteristics

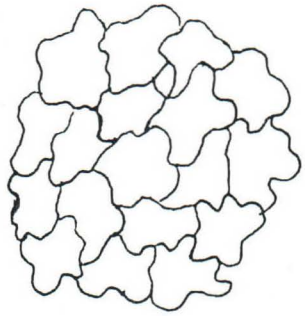
### Graminoids:

Grasses and related graminoids have a strict linear cell arrangement (Fig. 3a). Cells are arranged in two distinct zones in grasses: **costal**, or zone over the vascular tissue, and **intercostal**, or zone between vascular tissue Fig. 5). The costal zone is characterized by **silica** and **cork** cells or bodies (short cells), and **bristles. Long cells**, **stomata**, **guard** and **subsidiary cells**, **micro-hairs**, **macro-hairs**, or **bristles** are structures that may appear in the intercostal zone. Related graminoids, such as sedges of the family Cyperaceae, lack true costal and intercostal zones. True short cells are not found in other graminoids. However, bright spots that are easily confused with silica

a.



b.



c.

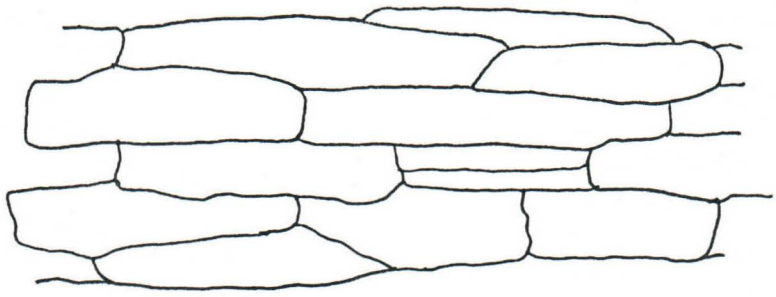


Figure 3. Basic plant cell arrangement patterns of graminoids (a), and forbs (b and c). a. linear b. irregular c. pseudolinear

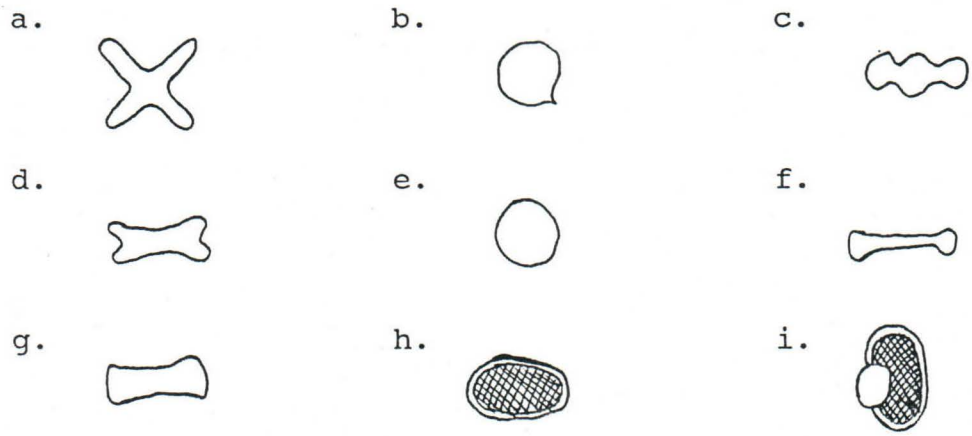



Figure 4. Short cell shapes (redrawn from Scott and Dahl 1980). a. x-shaped b. acute c. nodular d. crenate e. round f. thin bone-shaped g. thick bone-shaped h. cork cell i. silica cell embedded in cork cell

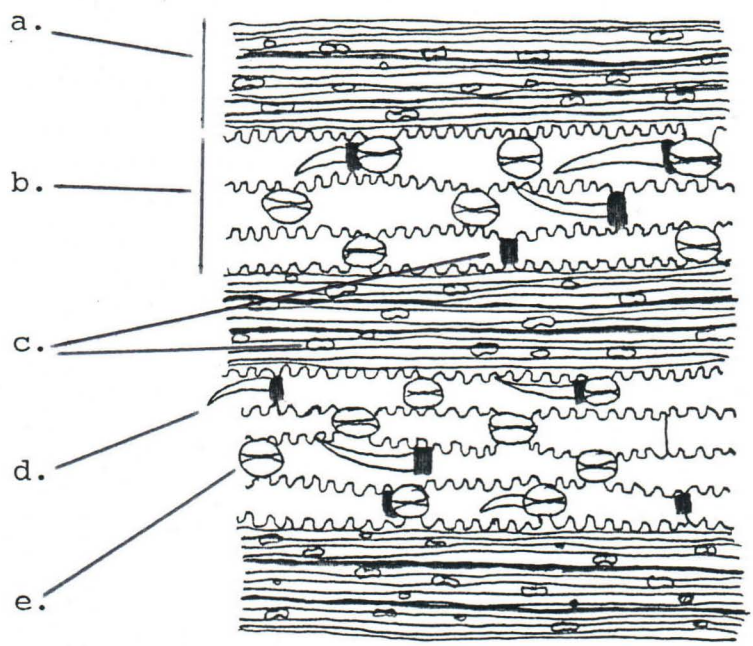



Figure 5. Epidermis of Deschampsia antarctica. a. costal zone b. intercostal zone c. short cells d. bristles e. stomata

cells do occur in some sedges (Scott and Dahl 1980).

**Short cells** are of two types: silica and cork. Shapes of short cells and their location in the plant epidermis are good diagnostic features (Fig. 4). Silica cells are indigestible and are readily identified in fecal material. They appear as bright spots due to refraction of light by the silica molecule. Cork cells are duller, more obscure, and sometimes occur in contact with silica cells.

**Long cells** of the intercostal zone may be quite variable in length, even in the same species. However, shapes of long cells can be used to distinguish among species (Fig. 6, 7). Number, shape, thickness, and degree of cell wall sinuations may also aid in identifying some species (Fig. 7).

**Micro-hairs** are multi-celled protrusions of the cell wall occurring in both costal and intercostal zones (Fig. 8b). They may assume a variety of shapes and compositions among plant species and can be used in plant identification.

**Macro-hairs** (or **trichomes**) are long, unicellular hairs occurring usually at leaf margins (Fig. 8c). Length and shape are relatively uniform among species. Though macro-hairs are sometimes used in identification, their usefulness is somewhat limited.

**Bristles**, also present in both costal and intercostal zones, are rounded or pointed, wide-based protrusions of

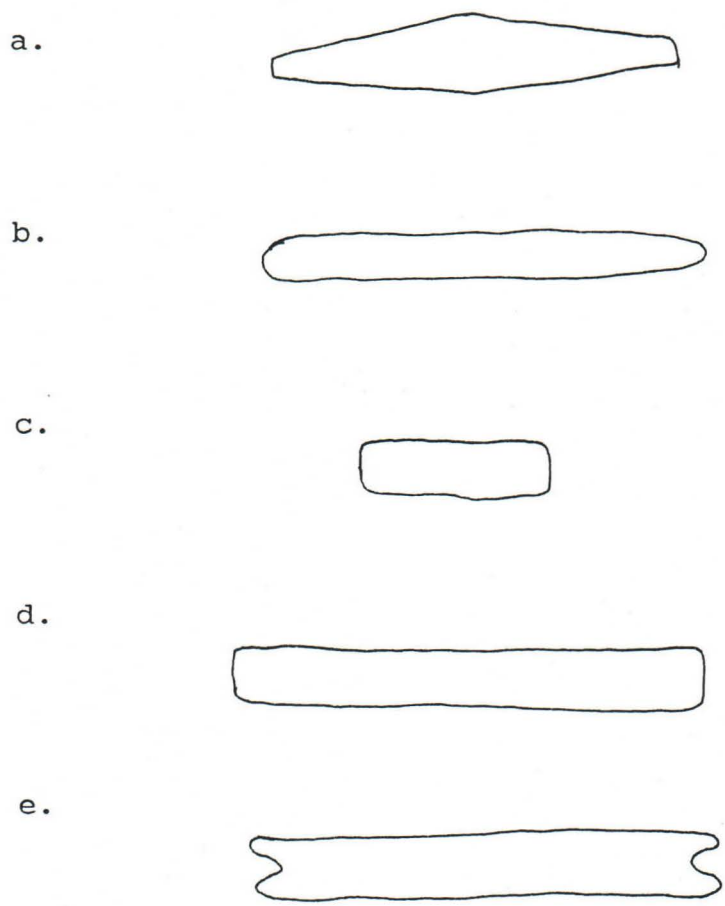



Figure 6. Long cell shapes. a. convergent b. parallel with rounded ends c. blocky short d. long e. crenate

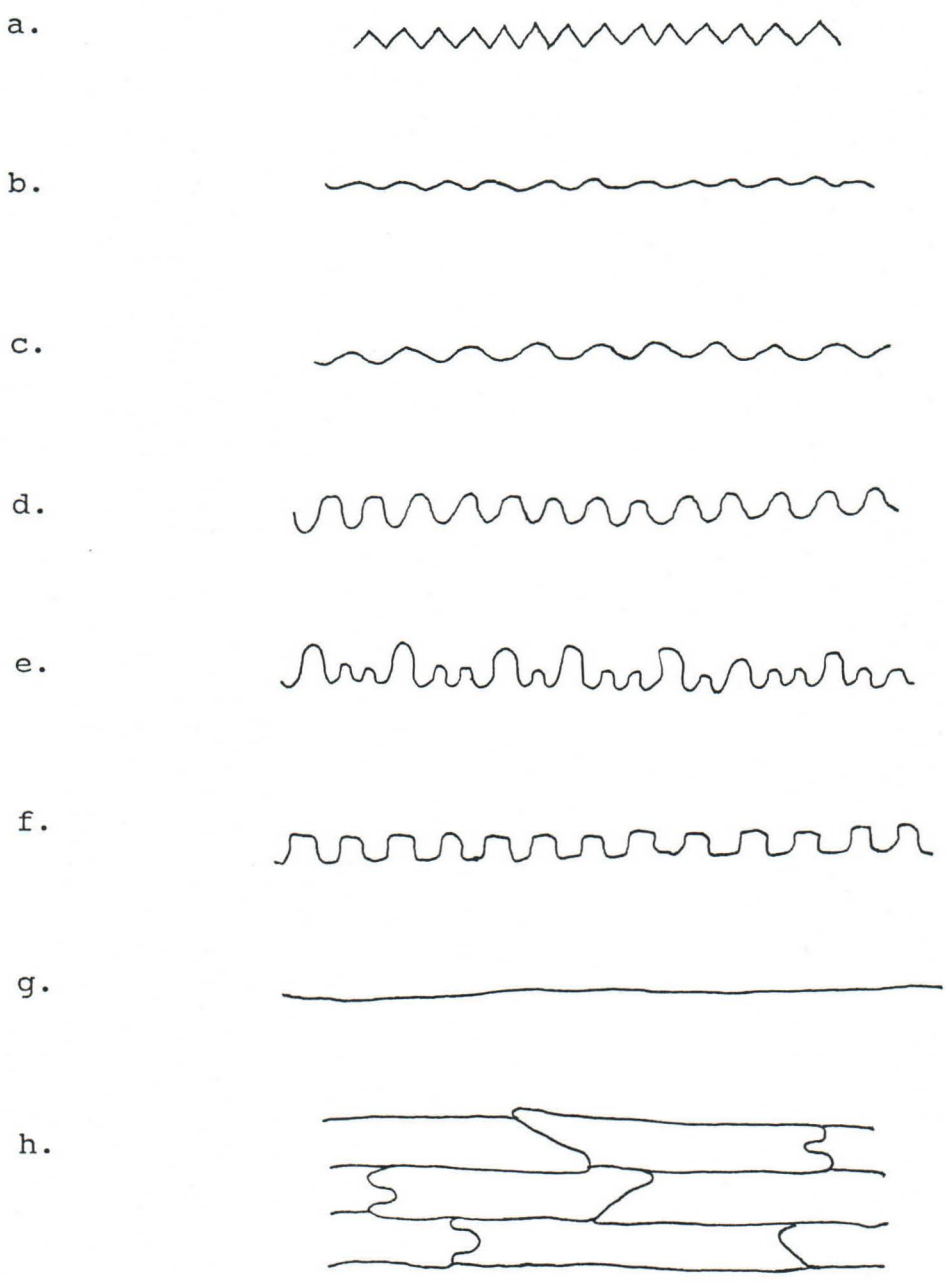
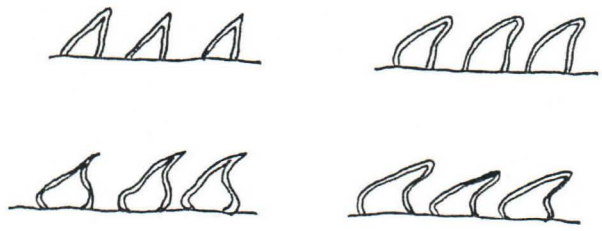
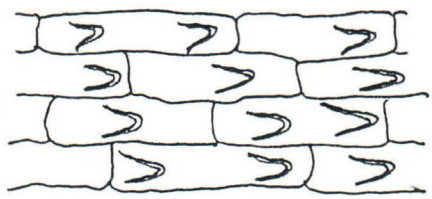



Figure 7. Cell wall patterns of long and short cells.
a. pointed b. shallow c. even d. deep
e. irregular f. square g. smooth
h. overlapping ends

a.



b.



c.

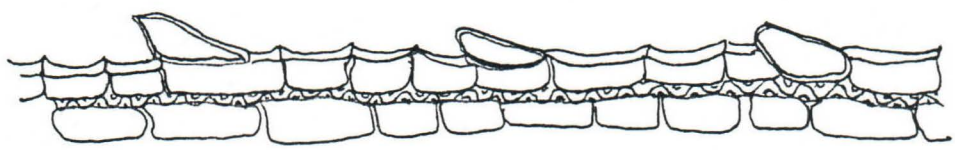


Figure 8. Bristles (a), microhairs (b), and macrohairs (c) of graminoids

cell walls (Fig. 8a). Bristles may also occur at leaf margins.

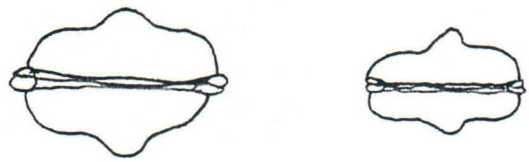
Stomata of grasses and their relatives are quite similar, possessing mature guard cells that are shrunken, appear as dumbbell-shaped structures, and are referred to as "graminaceous" (Fig. 9a, c, e, f)(Esau 1953). Graminoid stomata are classified as paracytic (Fig. 1d)(Scott and Dahl 1980, Metcalf 1960). Differences in stomata type may occur in some species and may be used in identification. Graminoid subsidiary cells often display marked differences in shape (Fig 9a, c, e, f). However, subsidiary cell shapes of grasses may vary due to distortions that occur in sample digestion or preparation (Scott and Dahl 1980).

Forbs:

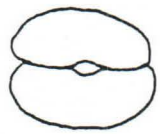
Unlike graminoids, forbs possess random or sometimes pseudo-linear cell arrangements (Figs. 3b and c, respectively). They lack short cells and do not possess costal or intercostal zones. Cell shapes and arrangement can also be useful in identifying forb species (Fig. 2).

Stomata and corresponding guard and subsidiary cells are often arranged in identifiable patterns (Metcalf and Chalk 1979, Esau 1953). Guard cells are usually larger and more rounded than in graminoids (Fig. 9b, d, g). Forb stomatal types are varied and are listed in Fig. 1.

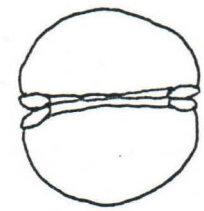
a. graminaceous, triangular guard cells



b. kidney shaped



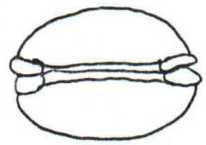
c. graminaceous, high-domed



d. half-moon shaped

e. graminaceous, parallel

f. graminaceous, low domed



g. crescent-shaped

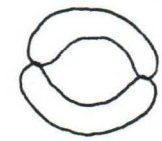


Figure 9. Various graminoid and forb stomatal types

Trichomes are common in most forbs, and can display unique patterns of number and shapes of cells, branching, points of attachment, or joint articulation. Many are multicellular (Fig. 10). Glandular trichomes, which are stalked with bulbous ends, are also observed and are diagnostic for some species (10e, f).

Woody plants (trees and shrubs):

Woody species are characterized by heavy pigmentation, high fiber contents, and kidney-shaped stomata (Fig. 9b). Within this broad group of plants, however, stomata are quite uniform and are not often diagnostic among species (Scott and Dahl 1980). Cell arrangement is similar to that of forbs, however cell walls tend to be thicker and more heavily pigmented. Many shrubs in the Torres del Paine region are also characterized by numerous epidermal lenticels and/or raised stomata.

Key

1. a. Cell arrangement linear, graminaceous guard cells.....Graminoids 2

b. Cell arrangement not linear, guard cells not graminaceous.....Trees, Shrubs, and Forbs 26

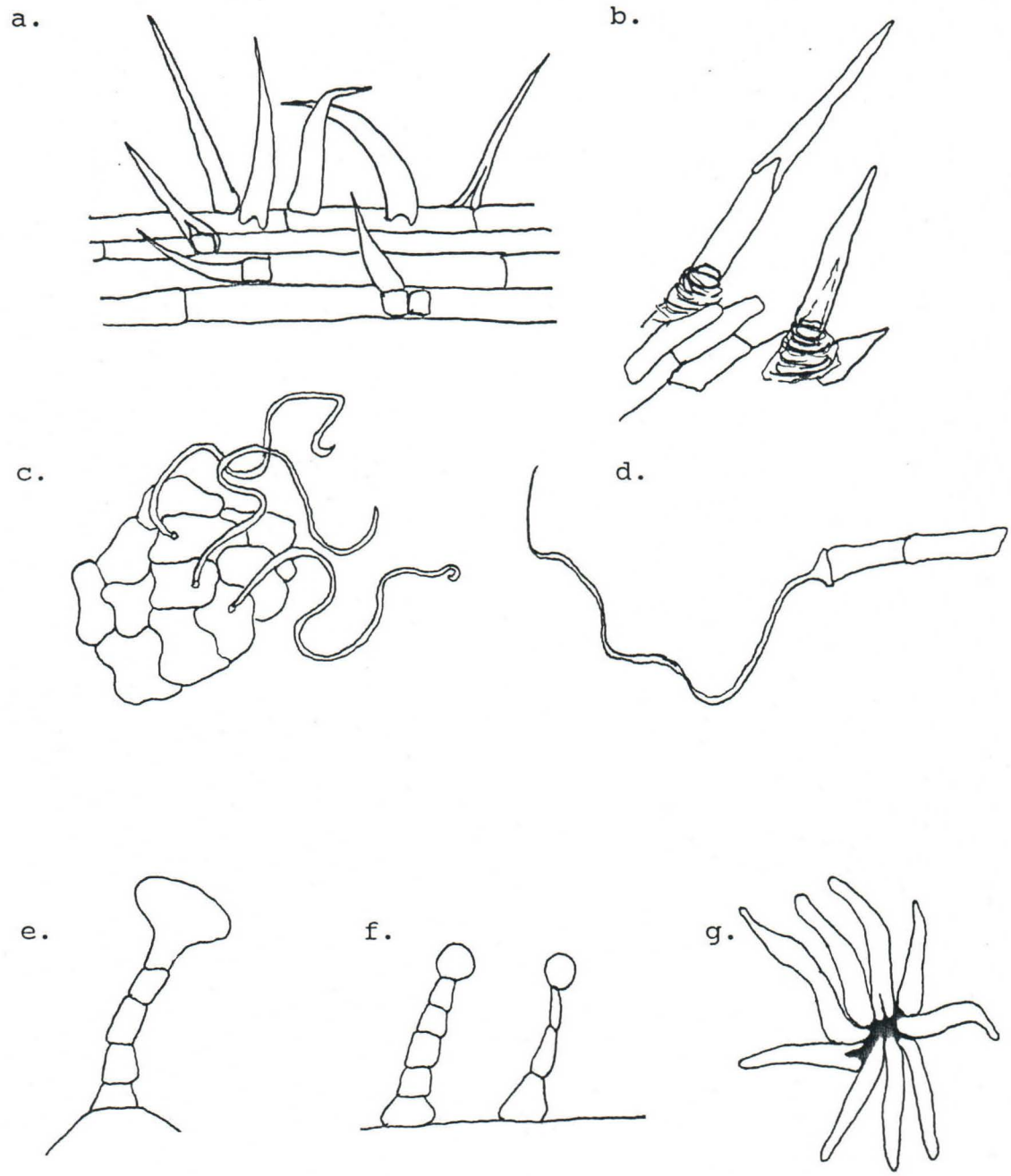



Figure 10. Trichomes of forbs. a. simple, unicellular b. simple, multicellular c. long, curly d. multicellular, filamentous e. glandular f. glandular g. stellate

2. a. True short cells present, costal and intercostal zones present and distinct.....Graminaceae 3

b. True short cells absent, costal and intercostal zones not distinct.....Cyperaceae 21

3. a. Branched silica bodies present..*Glyceria multiflora*

b. Branched silica bodies absent.....4

4. a. Silica cells "embedded" into crescent or slightly crescent-shaped cork cells.....5

b. Silica cells not embedded in cork cells.....17

5. a. Macrohairs present.....6

b. Macrohairs absent.....10

6. a. Long cell ends overlapping.....7

b. Long cell ends not overlapping.....9

7. a. Macrohairs long, $\geq$ 75$\mu$m, occasionally > 300$\mu$m, superficial with swollen bases.....*Hordeum comosum*

b. Macrohairs short, stiff, usually $\leq$ 75$\mu$m, bases not swollen.....8

8. a. Cell walls highly thickened, macrohairs present in intercostal zone only.....*Stipa humilis*

b. Cell walls not usually thickened, macrohairs present in intercostal and costal zones.....Poa trivialis

9. a. Cell walls highly thickened, macrohairs present in intercostal and costal zones.....Festuca gracillima

b. Cell walls normal, macrohairs present in costal zone only.....Trisetum tomentosum

10. a. Prickles present.....11

b. Prickles absent.....16

11. a. Prickles present in costal or intercostal zone, not present at margins.....12

b. Prickles absent in costal and intercostal zones, present in margins only.....19

12. a. Short cells are round.....13

b. Short cells are not round.....15

13. a. Short cells oblong, long cells overlapping.....Deschampsia antarctica

b. Short cells not oblong, long cells not overlapping.....14

14. a. Long cells parallel-sided or convergent, acute short cells, cell wall sinuations do not continue around stomatal subsidiary cells.....*Agrostis glabra*

b. Long cells parallel-sided only, no acute short cells, cell wall sinuations continue around stomatal subsidiary cells.....*Festuca magellanica*

15. a. Long cells parallel-sided or convergent, papillae present.....*Deschampsia venustula*

b. Long cells parallel-sided only, no papillae present.....*Alopecurus magellanicus*

16. a. Costal short cells dumbbell-shaped.....*Deschampsia caespitosa*

b. Costal and intercostal cells not dumbbell-shaped, but round.....*Phleum commutatum*

17. a. Short cells round, guard cells triangular, long cells $\leq$ 45 $\mu$m .....18

b. Short cells not round, guard cells not triangular, long cells $\geq$ 60 $\mu$m.....*Poa pratensis*

18. a. Costal short cells elongate and sinuous, prickles common.....*Phleum alpinum*

b. Costal short cells not elongated nor sinuous, prickles rare or absent.....*Agropyron fuegianum*

19. a. Long cells overlapping, crenate short cells.....*Agrostis capillaris*

b. Non-overlapping long cells, short cells round or cuboid.....20

20. a. Short cells elliptical or rounded, long cells parallel-sided or convergent, macrohairs present in margins, intercostal and costal zones.....*Holcus lanatus*

b. Short cells elongated with smooth undulations, long cells parallel-sided only, macrohairs present in intercostal zone only.....*Trisetum fluorescens*

21. a. Guard cells triangular, low-domed.....*Carex banksii*

b. Guard cells not triangular.....22

22. a. Long cell walls convergent.....23

b. Long cell walls parallel.....24

23. a. Long cells cuboid, shortened, with smooth sinuations.....*Carex darwinii*

b. Long cells elongated, not cuboid, sinuations not smooth, distinct.....25

24. a. Macrohairs present, 0-150 μm.....Eleocharis albibracteata

b. Macrohairs absent.....Juncus scheuzerioides

25. a. Macrohairs present, 0-75 μm.....Eleocharis pachycarpa

b. Macrohairs absent.....Carex gayana

26. TREES, SHRUBS, and FORBS

a. Cells highly pigmented, guard cells kidney-shaped.....27

b. Cells not pigmented, guard cells crescent shaped.....31

27. a. Stomata actinocytic.....Nothofagus antarctica

b. Stomata not actinocytic.....28

28. a. Stomata parallelocytic, enclosed by stomatal crypts.....Adesmia boronoides

b. Stomata anomocytic, not enclosed by stomatal crypts.....29

29. a. Cells rounded and angular.....*Senecio* spp.

b. Cells elongated and blocky.....30

30. a. Cell walls with large pits visible at 10x.....*Mulinum spinosum*

b. Cell walls with no pits visible at 10x.....*Berberis buxifolia*

31. a. Stomata abundant or readily seen.....32

b. Stomata rare or absent.....42

32. a. Pseudo-linear (regular) cell arrangement.....33

b. Nonlinear (random) cell arrangement.....43

33. a. Stomata anomocytic.....34

b. Stomata not anomocytic.....37

34. a. Stomata resemble graminaceous stomata.....*Triglochin concinna*

b. Stomata do not resemble graminaceous stomata.....35

35. a. Stomata among linear cells are paracytic.....*Taraxacum officinale*

b. Stomata among linear cells never paracytic.....36

36. a. Cells shapes blocky, papillae absent; trichomes rare, branched, and pigmented.....Erigeron patagonicum

b. Cell shape not blocky, papillae present; trichomes common, multicellular, bases composed of stacked round cells, not branched or pigmented.....Spergula spp.

37. a. Stomata diacytic.....38

b. Stomata not diacytic.....40

38. a. Stomata sunken, subsidiary cells are faint, interstomatal cell walls partially surround stomata, but do not meet.....Sisyrinchium patagonicum

b. Stomata not sunken, subsidiary cells are well defined, interstomatal cells have no special characteristics.....39

39. a. Trichomes multicellular, long, thick-walled, curved.....Colobanthus specitensis

b. Trichomes unicellular, short, thin-walled, straight.....Taraxacum officinale

40. a. Stomata paracytic, guard cells not kidney-shaped.....41

b. Stomata laterocyclic, guard cells kidney-shaped.....*Azorella trifurcata*
*Azorella caespitosa*

41. a. Stomata raised and distinct, guard cells half-moon-shaped, trichomes multicellular with stacked round cells forming the base.....*Cotula scariosa*

b. Stomata normal, guard cells crescent-shaped, trichomes simple.....*Vicia magellanica*

42. a. Stomata present, apparent.....*Acaena magellanica*

b. Stomata absent or unapparent.....*Acaena pinnatifida*

43. a. Stomata actinocytic.....44

b. Stomata not actinocytic.....45

44. a. Trichomes abundant, multicellular, with bone-like articulations.....*Cerastium fontanum*

b. Trichomes rare, unicellular, simple.....*Triflolium repens*

45. a. Stomata anisocytic.....*Euprasia antarctica*

b. Stomata not anisocytic.....46

46. a. Stomata anomocytic.....47

b. Stomata not anomocytic.....56

47. a. Trichomes present.....48

b. Trichomes absent.....54

48. a. Papillae present.....Gentianella magellanica

b. Papillae absent.....49

49. a. Simple trichomes unicellular, tips angular and acute.....50

b. Simple trichomes multicellular, tips long and filamentous.....Gamochaeta nivalis

50. a. Trichomes abundant.....51

b. Trichomes rare.....Triflolium repens

51. a. Cell shapes blocky.....52

b. Cell shapes not blocky.....53

52. a. Stomata faint, guard cells in two distinct halves, cell walls smooth, trichomes curved and flexible.....Potentilla anserina

b. Stomata well defined, cell walls smooth or dentate, trichomes straight.....Geranium magellanicum

53. a. Cell walls jigsaw-shaped, trichomes medium length (50-75 $\mu$m), thick walled, straight...*Ranunculus peduncularis*

b. Cell walls angular, trichomes long ($\geq$ 76mm), thin, curled.....*Antennaria chilensis*

54. a. Cell walls blocky or angular.....*Rumex acetosa*

b. Cell walls not blocky or angular.....55

55. a. Cell shapes irregular with non-rounded corners.....*Hippuris vulgaris*

b. Cell shapes not irregular, round.....*Samolus spatulatus*

56. a. Stomata paracytic.....*Galium aparine*

b. Stomata not paracytic.....57

57. a. Papillae present.....58

b. Papillae absent.....59

58. a. Multicellular trichomes with cap-like tips.....*Arenaria serpens*

b. Multicellular trichomes, if present, without cap-like tips.....*Colobanthus quitensis*

59. a. Trichomes glandular.....*Madia sativa*

b. Trichomes not glandular.....60

60. a. Trichomes straight, thin, jointed.....*Calceolaria biflora*

b. Trichomes curved, thick, not jointed.....*Cerastium arvense*

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